THE PHYSIOGNOMY OF INSECTS

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Ante omnia scire convenit naturam corporis, quia alii graciles, alii obesi sunt; alii calidi, alii frigidiores; alii humidi, alii sicciores; alios adstricta, alios resoluta alvus exercet. Raro quisquam non aliquam partem corporis imbecillam habet.—Celsus, Lib. I. Cap. III.

AN ENTOMOLOGIST no less interested in his fellow men than in the insects may with increasing years of observation find increasing resemblance between the two—some insects seeming almost human and some humans behaving very much like insects. This may be due in part to the fact—if indeed it be a fact—that the entomologist may come to resemble the objects with which he is so constantly occupied. If we can trust the statements of some observers, he may even take on some of the physical peculiarities of the group in which he specializes. We have all known entomologists who looked like grasshoppers, cockroaches, bumble-bees or Histerid beetles. The confusion is increased by the fact—and this has not escaped the cartoonists—thar there is a certain resemblance between the human and insect body, with its division into head, thorax, and abdomen. And although the insect body has too many appendages and certainly too many wings to suit any human being this side of Paradise, nevertheless the face, head, and eyes of some Orthoptera, Coleoptera, Hymenoptera, and Diptera are very suggestive of certain physiognomies which we daily encounter in the streets and trolley-cars of our great cities. In certain ancient entomological works, purporting to be of a serious character, for example in Jonston's *Theatrum universale omnium animalium* (1718), the heads of insects are often drawn with the obvious intention of accentuating their resemblance to human countenances.

HUMAN TYPES

Those who devote all their attention to our own highly polymorphic species, which Linnæus, I suspect, somewhat sarcastically called *Homo sapiens*, have repeatedly endeavored to group its various individuals in categories according to their temperaments and physical peculiarities. As a result, a number of human types have been distinguished and named

by a long series of investigators, most of whom agree that the pure types are best studied among the young adult males of the species. Two of the types, which have been recently called the "asthenic" and the "pycnic" by Kretschmer (1922), stand out conspicuously and will be recognized at once by the following diagnoses:

The asthenic is pale, scrawny, long-limbed, with narrow head and face ("hatchet-faced"), long, narrow, straight nose, small, often receding chin, narrow chest and abdomen, deficient development of fat and musculature, reduced pilosity on the body but often with abundant cranial thatch, abstemious, dyspeptic, with a tendency to tuberculosis, and when insane, schizophrenic, i.e., prone to fixed ideas, ideas of persecution, etc. This type is active, intense, intellectual, self-centered (introverted), often deficient in a sense of humor, fond of reforming, dogmatic or fanatical, and not infrequently detestable when claiming a too intimate knowledge of the Almighty's plans for making the world safe for democracy. The pycnic—so called, not because he likes picnics, though no other type is so fond of them—but from the Greek word πυκνός, meaning compact or thickset—is rubicund, rotund, large-bodied, short-limbed, broad through the chest, but broader through the abdomen, with round or pentagonal face, pug or thick nose, moderately pilose, fond of eating and drinking, eupeptic, with a tendency to apoplexy and arteriosclerosis; on the mental side cyclothymic, i.e., predisposed to the recurring, circular or manic-depressive forms of insanity, such as melancholia; extroverted, socially easy-going, tolerant in morals and religion and often very lovable because claiming no inside information in regard to the Almighty's designs.

These two types in their purity are sufficiently frequent among our American population. Kretschmer seems to have found the pycnics very common among the Swabians, who are generally characterized by the Germans as "gemütlich" or "gutmütig." The popular distrust of the asthenic and fondness for the pycnic is indicated by the fact that Satan, or Mephistopheles is usually represented as an asthenic while the favorite gods and saints of China and Japan are depicted as fat pycnics. When the belief in Satan was more vigorous than it is at present, he and his demons were often represented as belonging to the athletic type. [See the pictures from the twelfth to the sixteenth century and especially the frontispiece from Didron's *Christian Iconography* in Bonner (1913)]. Why the people should have chosen a symbol like Uncle Sam to represent the United States and one like John Bull to represent England was not altogether clear till the passage of the Volstead Act. Among historical figures the reader will recall Cassius (as depicted by Shakespeare), Dante, Savonarola, Torquemada and John Calvin as asthenics and Falstaff (as conceived by Shakespeare), Martin Luther and ex-President Taft as pycnics. In fiction Don Quixote and Sancho Panza are good examples of the two types. Bud Fisher's creation of Mutt and Jeff may also be cited in this connection.

The great mass of human individuals, however, may be regarded as blends or mosaics of the two types in varying proportions. Even during the lifetime of the same individual, the asthenic may predominate at one time, the pycnic at another. Often the young are asthenic and become pycnic with advancing years, and we have all seen examples of the reverse transformation of pycnic youngsters into asthenic oldsters. Undoubtedly the endocrine glands, and especially the thyroid, pituitary and interstitial glands,

are concerned in the production of both the extreme and the intermediate types.

Among the latter Kretschmer recognizes several categories. One of these is the "athletic," which I need not describe as the reader is familiar with its physical and mental peculiarities from the football and baseball field, the gymnasium, vaudeville stage and movies. Kretschmer further distinguishes "dysplastic" types, which show more or less pathological defect- or excess-development (hypoplastic or hyperplastic development) in certain characters, but I shall pass over these distinctions and for the sake of brevity and clearness call all the intermediates athletic.

The same or similar types have been recognized by other investigators and have been reviewed by Bauer (1924). The asthenic, athletic and pycnic types of Kretschmer evidently correspond to the phthisic, athletic and plethoric habitus of de Giovanni and to Beneke's microsomatic, microplastic, microskelic, longi-

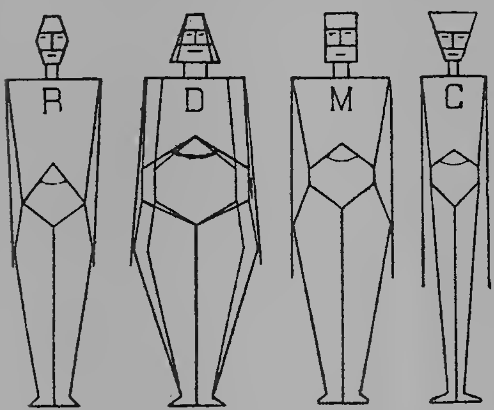

Fig. 1. The Four Human Types of Claude Sigaud, Schematized by Pierre Robin

lineus or longitypus and megalosomatic, euryplastic, brachyskelic, brevilineus or brachytypus, with the intermediate normosplanchnic, normosomatic, mesoplastic, normolineus, normotypus. The two extreme types correspond to Viola's microsplanchnic, or phthisic habitus and megalosplanchnic, or apoplectic habitus, to Bryant's carnivorous and vegetarian

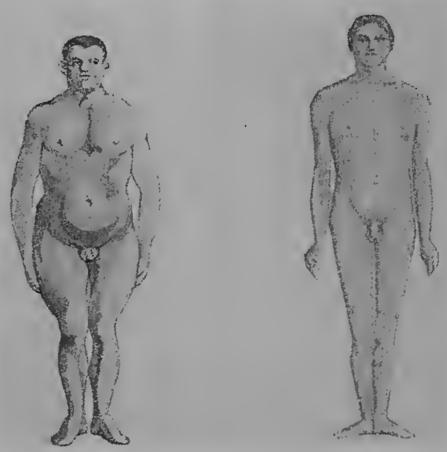

Fig. 2. Idealized "Round" and "Flat" Colloidal Human Types, According to MacAuliffe (Taken from A. Thooris: *La vie par le Stade*)

types, Bean's hypermorph and mesomorph types, Stockard's linear and lateral types, etc. Obviously the pycnic type is that of the human infant. According to Stockard (1923) "the linear type is the faster growing, high metabolizing, thin but not necessarily tall group, while the lateral type is slower in maturing and is stocky and rounder in form."

The French school, following Sigaud and including his pupils Chaillon, MacAuliffe and other contributors to the very interesting *Bulletin de la Société d'Etude des Formes Humaines*, recognize four human types, the respiratory, digestive, muscular and cerebral (fig. 1). The digestive corresponds to the pycnic, the cerebral to the asthenic, the muscular and respiratory to the athletic type of Kretschmer. In a recent paper MacAuliffe (1925) distinguishes a "round" and a "flat" type (fig. 2), which correspond to the pycnic and asthenic respectively, and refers their differences to differences in the col-

loidal state of their tissues, the former consisting of strongly, the latter of feebly hydrophilous gels. The cells of the bibulous pycnic have great osmotic powers, those of the asthenics a feeble surface tension. "The flat type functions more economically than the round. It is also probable that the electric polarization of the cellular surfaces is higher in this latter human category."

Bauer studied the distribution of Sigaud's four categories among 2000 male Viennese and found the following proportions of pure type: respiratory 18 per cent,

Fig. 3. Heads of Grey Hound, Bittern, and Pike to Illustrate the "Flat" Colloidal Type of MacAuliffe
(Taken from A. Thooris: *La vie par le Stade*)

muscular 9 per cent, cerebral 3.9 per cent, digestive 3.8 per cent. Taking the mixed forms in which one of the types predominates, he found: respiratory 43.1 per cent, muscular 23.8 per cent, cerebral 18 per cent, digestive 6.6 per cent. The remaining 8.5 per cent could not be included in any one of the categories. Zweig, one of Bauer's students, studying the same material disproved Sigaud's view that the types do not change with age, although it was clear that each is fixed in youth in its general characters. The digestive type increases with age. Sigaud's schema is not easily applicable to females. Bauer divides them according to the distribution of fat on their bodies into (1) "Reithosentypus" (with fat on hips); (2) fat on arms, breast and neck, but with thin legs; (3) fat on thighs and legs, but poorly developed on trunk; (4) fat on breasts and gluteal region (steatopygous type).

ANALOGUES OF HUMAN TYPES AMONG ANIMALS

Now it is interesting to note that all the main types exhibited by the single species *Homo sapiens* have their analogues in most groups of animals and even among the plants. As examples of the asthenics and pycnics I mention only the following: among our domestic animals the greyhound and King Charles spaniel (figs. 3 and 4) and among other mammals the giraffe and armadillo, among the birds the herons and finches (figs. 3 and 4), among reptiles the tree-snakes and box-tortoises, among the amphibians the coecilians and toads, among fishes the eels and box-fishes; among crustaceans such forms as *Caprella* and the crabs; among Echinoderms the brittle-stars and the sea-urchins; among myriopods *Geophilus* and *Glomeris* and among plants the vines and the melon-cacti. Between the extremes in each case we find the great majority of species, the athletes, which exhibit a more nearly average development of their organs.

Of course, the insects, which are represented on our planet by such a bewildering number and variety of highly specialized species, may be expected to show the asthenic and pycnic types in a very pronounced form. There are, in fact, in all the principal orders, whole genera or even families of the two types. For purposes of illustration I have brought together a series of these insect Mutts and Jeffs in the accompanying figures (figs. 5 and 6).

As the reader is familiar with them or with similar forms I shall not stop to designate the various tenuous walking-sticks, grasshoppers, ants, dragon-flies, crane-flies, mosquitoes, ant-lions, panorpids, etc., nor the many chunky bugs, beetles, moths, etc. The reader will notice that the latter insects, like some human pycnics, have large rotund bodies and rather short, slender legs, and will recall certain ently and often unsuccessfully wrestling with them, will certainly not object.

The general impression produced by the insect asthenics and pycnics is that of mutations which have somehow managed to survive among the great mass of athletic species, but it is doubtful whether they have arisen as such saltatory variations. The asthenics are more archaic or at least more frequent in ancient and

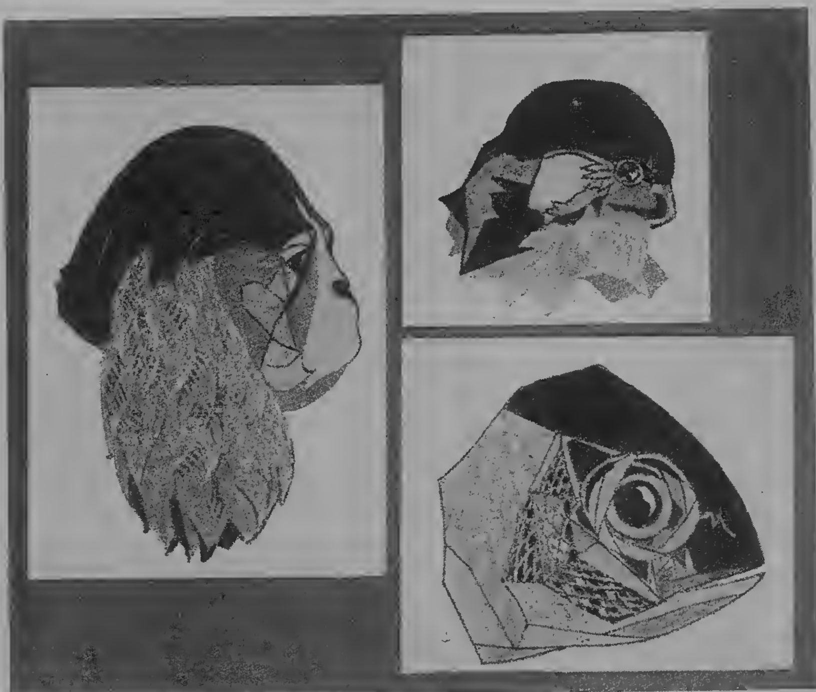

Fig. 4. Heads of King Charles Spaniel, Finch, and Bream, to Illustrate the "Round" Colloidal Type of MacAuliffe
(Taken from A. Thooris: *La vie par le Stade*)

cases of both types occurring in succession in the same species, as, e.g., in the ant-lion, which has a pycnic larva and an asthenic adult, and the flea which has an asthenic larva and a rather pycnic adult. Among the insects, too, the great majority of species are intermediate, and if I designate this group as "athletic" the economic entomologists, who spend their lives ard- primitive orders or suborders, and, with the exception of the mosquitoes and Chironomids, seem often to belong to rather rare, recessive or evanescent species. The differences between the two types cannot be due to the quality of the food, because there are predatory and phytophagous species in both groups. That they differ in metabolism is probable.

The pycnics, like their human analogues, are certainly great feeders compared with the asthenics—compare, e.g., the appetite of a dung-beetle with that of a walking-stick insect. And structurally there is a great difference in musculature, the muscles of the asthenics being long and slender while those of the pycnics are short and voluminous. This matter of the musculature in these and other insects—a matter as much neglected by recent insect morphologists as it was emphasized by those of former times—I should like to place in the center of the following discussion, because, as we shall see, it is the musculature that mainly determines the physiognomy of insects.

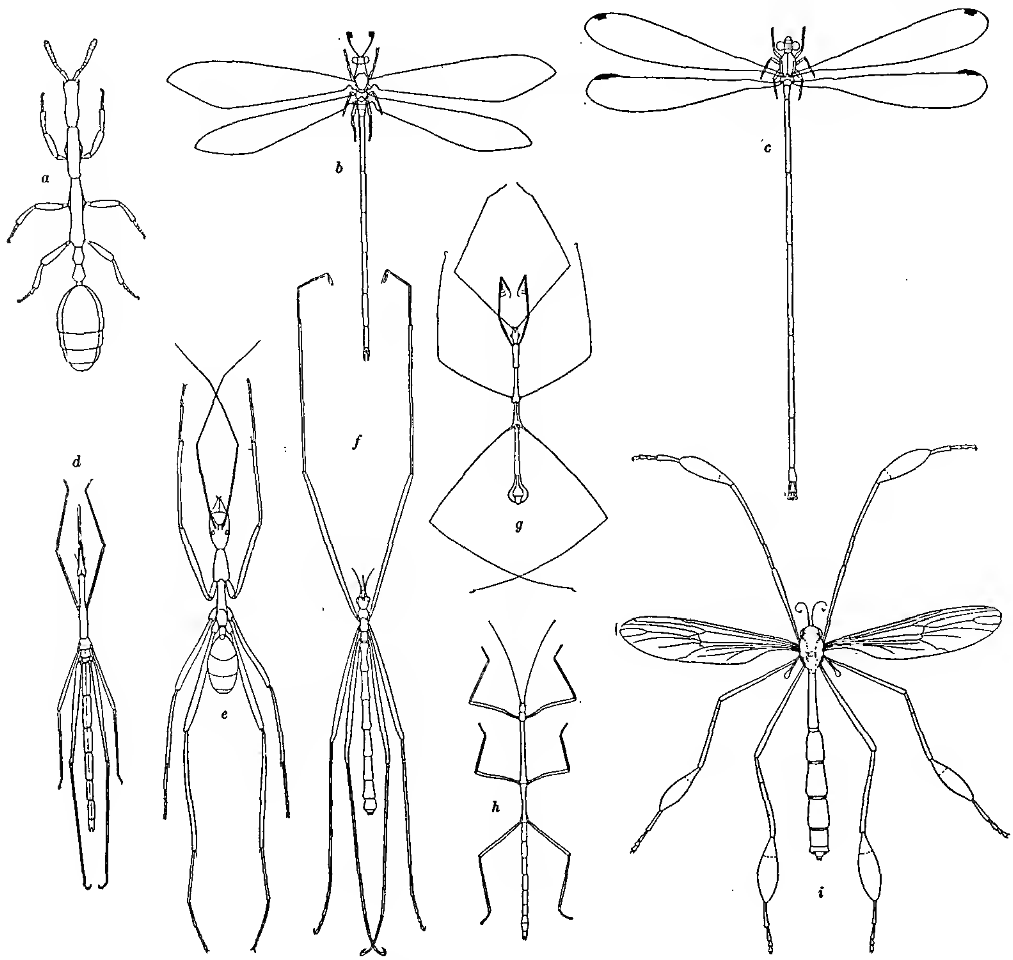

Fig. 5. Examples of Asthenic Insects Belonging to Various Orders
a, Staphylinid myrmecophile (Coleopteron); *b*, ant-lion (Neuropteron); *c*, dragon-fly (Odonate); *d*, grasshopper (Orthopteron); *e*, ant (Hymenopteron); *f*, Panorpid (Mecopteron); *g*, bug (Heteropteron); *h*, Phasmid (Orthopteron); *i*, crane-fly (Dipteron).

PRINCIPLES OF INSECT PHYSIOGNOMY

The reader is familiar with the fact that in insects, as in other arthropods, the musculature is inside the skeleton to

which it is attached and that the shape and size of the various elements of the skeleton depend on the volume and arrangement of the muscles. Here the skeleton and integument are one, whereas in vertebrates the muscles which move the skeletal elements are external to them and immediately beneath the very flexible integument. Hence in vertebrates that are not too scaly, feathery or hairy the play of the musculature is visible from the outside, whereas in insects we are presented with a rigid envelope capable of movement only at well-defined, preformed articulations. Hence, also, the very limited and mechanical expression of the emotions in insects as compared with the wonderful range and subtlety of expression in the human face and body, a range and subtlety so extraordinary that from

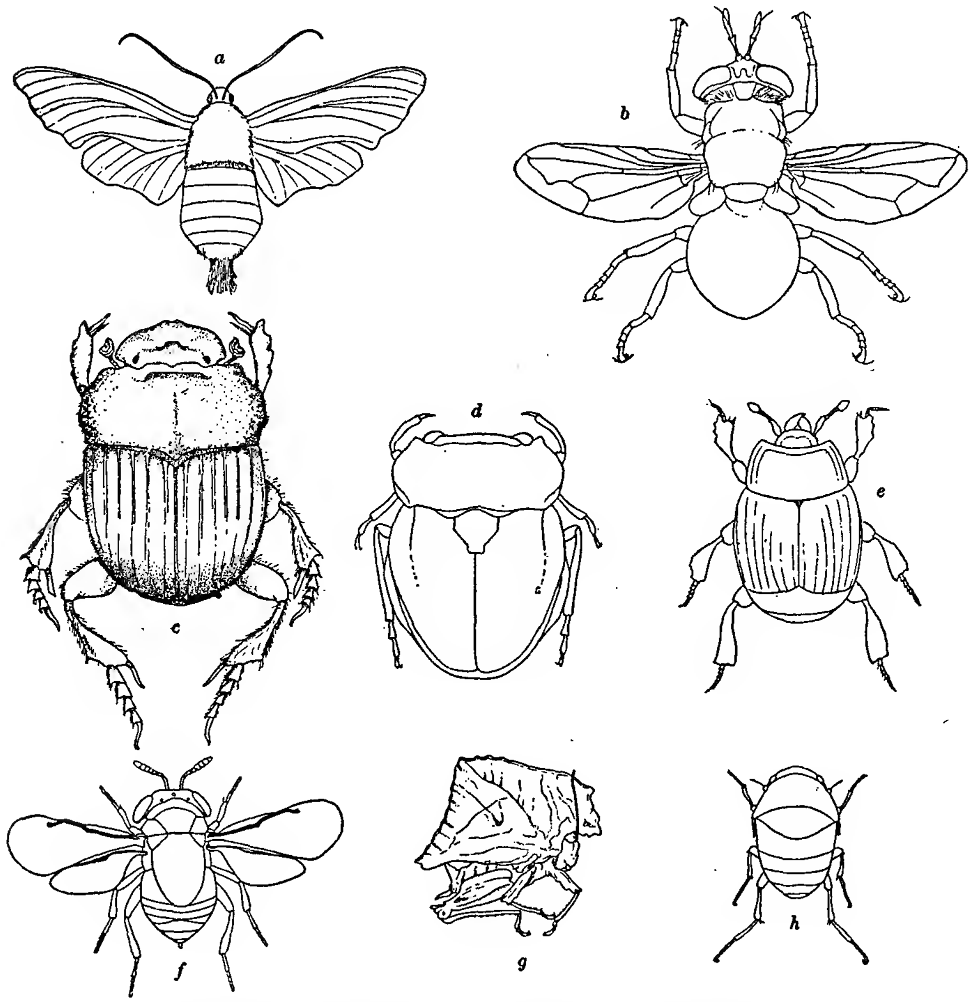

FIG. 6. EXAMPLES OF PYCNIC INSECTS BELONGING TO VARIOUS ORDERS

a, Sphingid moth (Lepidopteron); *b*, Syrphid fly (Dipteron); *c*, Lamellicorn beetle (Coleopteron); *d*, bug (Heteropteron); *e*, Histerid beetle (Coleopteron); *f*, Chalcidid fly (Hymenopteton); *g*, grasshopper (Orthopteron); *h*, Phorid fly (Dipteron).

our earliest years it constitutes a means of intercommunication among us second only and very often superior to articulate speech. Moreover, although the powers of facial and bodily expression of the human infant are very limited compared with those of the adult, as we should see if we could follow the development of some great actor from his birth to his highest triumphs on the stage, the insect's expression throughout each of its instars is extremely uniform and circumscribed. Of course if we could look

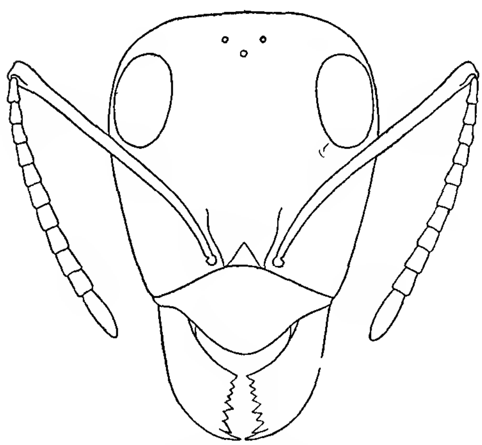

Fig. 7. Head of Worker of the Common Circumpolar *Formica fusca* L. from Above, Showing Eyes, Ocelli, Antennæ, Clypeus and Mandibles

beneath the rigid chitinous integument of such insect busybodies as ants, bees or solitary wasps we should probably witness an astonishing wealth of expression in the finer play of the smaller muscles, especially of those belonging to the viscera.

To trace the correlations between the development of the various muscles and that of the skeletal elements throughout the insect body would prove to be an undertaking as formidable as it would be wearisome. I shall therefore discuss at length only the most interesting region, the head, and confine myself still further very largely to a consideration of the ants. This will be best for two reasons: first, because I have been peering for nearly thirty years into the countenances of so many thousands of these insects that I have acquired some familiarity with their idiosyncracies, and second, because they are unusually favorable for physiognomic studies, owing to the extraordinary morphological and functional differences between the sexes and castes of the same species. The reader will have no difficulty in testing the general validity of my conclusions by extending them to the insects of other families with which he is acquainted.

The following are the main points which I should like to establish:

1. The form of the head and face is very largely determined by the size and shape of the flexor muscles of the mandibles and in turn the functional or adaptive peculiarities of these organs are closely correlated with the character of their flexor muscles.

2. In certain species, at least, the development of the antennal muscles seems to be correlated with the convexity of the front, or forehead.

3. The antennæ are also responsible for the development of certain adaptive structures in the configuration of the head, such as the scrobes.

4. The eyes are of little importance in determining the shape of the head in the workers and females of most ants, but these organs, when large, as in male ants and especially in certain other insects with haustellate mouthparts (Diptera, Lepidoptera, Mecoptera, Heteroptera, etc.) have considerable physiognomic value.

5. Certain head-forms are very largely determined by direct adaptation to the cylindrical cavities in the hard plant tissues or soil inhabited by the insects.

Let us begin with the head of our common *Formica fusca*, an ant of the true Nordic type, the *beau ideal* of the family, with chaste, well-balanced features and beautifully rounded forehead (fig. 7). To a slightly stretched imagination this head will not appear so very inhuman, especially if we let the clypeus represent the nose. The mouth is rather large, to be sure, and its upper lip is hidden away under the clypeus. The antennæ and mandibles, however, are decidedly inhuman. But if we imagine our hands and arms split into two pairs of appendages, and one pair thin, mobile, covered with exquisite, intermingled tactile and olfactory organs and inserted just above the base of our nose, and the other, shortened till only the rigid hands remain and inserted in the corners of our mouth, we should be equipped very much like an ant. And, no doubt, we should find the whole arrangement delightfully convenient. We could do very rough work with our inferior, or oral pair of hands without in the least impairing our sense of touch in the superior, or nasal pair, and the intimate combination of touch and smell in this pair would enable us to gain a very satisfactory knowledge of our immediate environment. We should move through the world like ants, continually topochemorecepting the various objects in our path, and we should probably speak of strawberries as soft, rounded-conical odors, of cigarettes as harder, cylindrical odors, table-tops as very hard, smooth, oblong odors of a certain quality, etc.

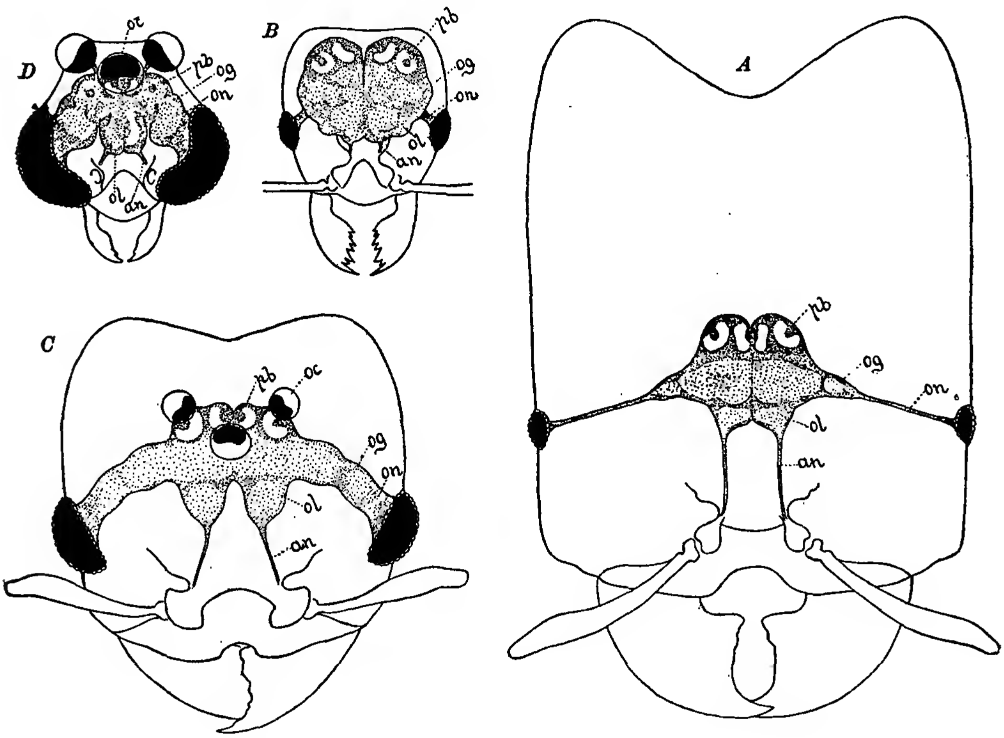

FIG. 8. HEADS AND BRAINS OF THE FOUR CASTES OF *Pheidole instabilis* EMERY FROM TEXAS, DRAWN TO THE SAME SCALE

A, soldier; *B*, worker; *C*, female; *D*, male

Judging by superficial appearances we might be tempted to extend the old phrenology of Gall and Spurzheim to the ant and regard the size and shape of its hard cranium as indications of the size and shape of its brain, but when we open its head we see at once that the brain is separated by a considerable space from the cranial wall and that the greater part of the cranial cavity is filled with muscular tissue. The brain varies greatly

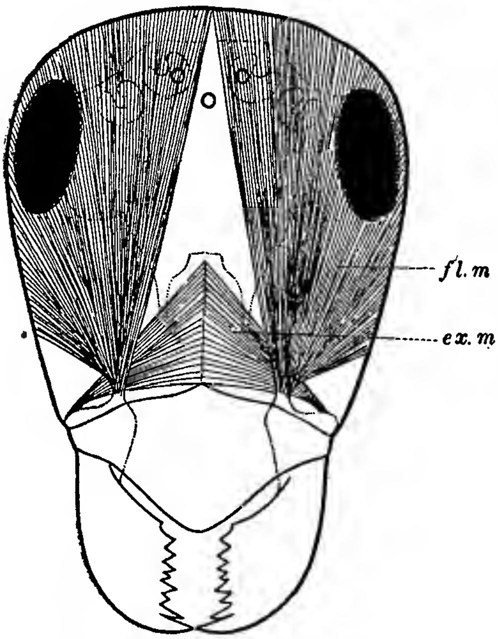

FIG. 9. HEAD OF WORKER *Formica fusca* L.
fl. m., flexor muscle of mandible; *ex. m.*, extensor muscle of same.

in different species and even in the different castes of the same species. Roughly speaking, the brain seems to vary inversely as the size of the individual ant. This is clearly seen in the heads of the four castes of a common Texan *Pheidole* (*Ph. instabilis*) (fig. 8). When the eyes are small or of moderate size, therefore, the head is an index to the muscular powers and not to the intelligence or sensory development of the insect.

CORRELATION OF HEAD SHAPE AND MUSCULATURE OF MANDIBLES

Returning to the head of *Formica fusca* (fig. 9) which has an unusually large brain, and removing the dorsal wall, we observe that on each side of the median line its contents consist very largely of a huge pyramidal muscle, which is attached proximally by a short, stout tendon to the inner corner of the base of mandible, while the gradually expanding fibres are attached distally to a very large area comprising much more than the posterior half of the cranial wall. In some ants this muscle, the contraction of which closes the mandible, really consists of two muscles, but as both have the same mandibular tendon and the same function, I shall treat them as a unit. It has been called the adductor, or flexor mandibulæ. The muscle which opens the mandible, the abductor, or extensor, is very much smaller. It is flattened and fan-shaped, inserted by a short, stout tendon on the outer corner of the extreme base of the mandible and runs ventrally under the tendon of the flexor to spread out and become attached to a thin, chitinous plate, or apodeme, which rises in the middle line from the floor or ventral wall of the cranium, the gula.

The great differences in the volume of the mandibular flexors and extensors is, of course, correlated with differences in their functions. The extensors have merely to open the mandibles, but the flexors have to perform the much more arduous task of seizing, holding, biting, gnawing or crushing the prey or the wood or soil in which the ants' nests are made. We may, therefore, concentrate our attention on this pair of more important muscles, whose development in the various species and castes intimately depends on the structure of the mandibles, and since the mandibles

differ greatly according to the habits of the ants it will be advisable to consider these appendages somewhat more closely. The typical mandible has a three-cornered blade, with a straight or more or less convex, entire outer border and two straight inner borders, one basal and toothless, the other apical and armed with teeth. A great many different types of mandibles may be recognized among the Formicidæ, but I will reduce them to nine: first, *biting* mandibles, of moderate size, very long, slender, with long apical border, armed with a few or numerous often unequal teeth (fig. 13–15); sixth, *clipping* mandibles, which are long, linear, straight or slightly curved, with a few sharp, abruptly incurved teeth at the apex, and the inner borders toothless, or finely serrate (figs. 16 and 17); seventh, *piercing* mandibles, which are slender, sickle-shaped and pointed, without teeth or with minute vestiges of them along the inner border (fig. 18*e*–*h*); eighth, *vestigial*

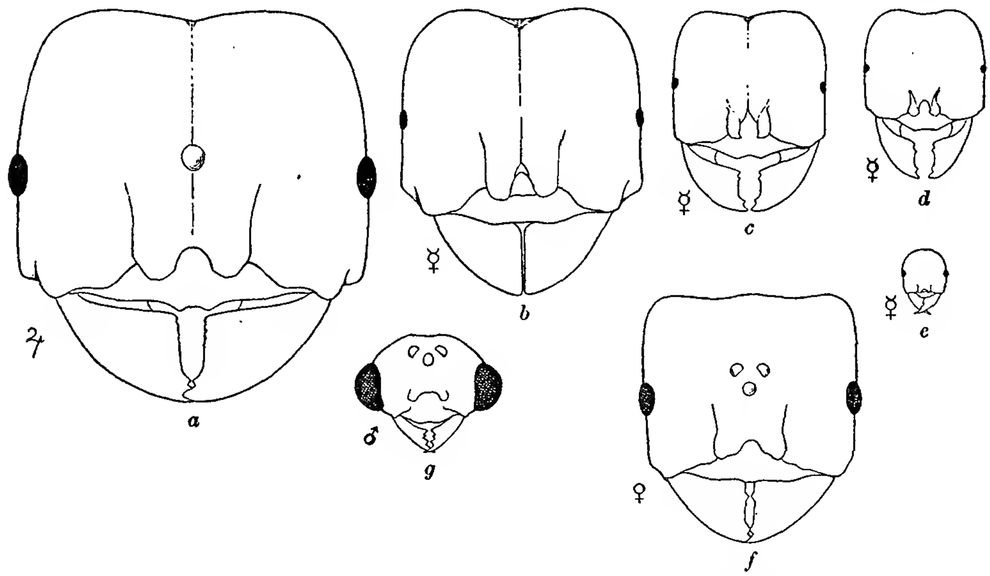

FIG. 10. HEADS OF VARIOUS CASTES OF AN EAST INDIAN HARVESTING ANT, *Pheidologeton diversus* JERDON
a, soldier; *b* to *d*, intermediate forms between the soldier and worker minima, *e; f*, female; *g*, male. Note rounding of occiput correlated with feeble mandibular development in the male and minima.

with subequal internal borders and a moderate number of sharp teeth on the apical border (figs. 7, 9, 12); second, *gnawing* mandibles, which are short and stout, with a few broad, strong teeth (fig. 12*a*); third, *crushing* mandibles, which are thick and stout, very convex externally, with few or no teeth (fig. 8a, 9a–d); fourth, *cutting* or scissor-like mandibles which are broad, flat and rather thin, with sharp, toothed apical border (fig. 11); fifth, *grappling* mandibles, which are mandibles which are reduced and apparently useless organs, occurring only in the male sex (figs. 10g and 17*b*); ninth, *aberrant* mandibles, including a number of singular forms of still unknown function (figs. 19 and 20). Of these various types, the biting, gnawing, crushing and cutting mandibles are large and powerful; the grappling, piercing, clipping, vestigial and aberrant though sometimes of large size are rather weak and therefore furnished with less powerful flexor muscles.

We may now examine several examples which show very clearly the correlation between the size and development of the mandibles, their flexor musculature and the shape of the head, a correlation so intimate that an expert mathematician might be able to express it in definite formulæ. In figure 21 I have represented the various castes of the harvester, *Pheidole instabilis*. The large individual and collects the seeds and stores them in the nest. The big-headed forms may be called the official nut-crackers of the colony because they crush the seeds with their mandibles. You will notice that the head decreases in size and length and in the convexity of its occipital lobes, as indicated by the gradual rounding of the posterior corners and decreasing concavity of the occipital border, till we reach the

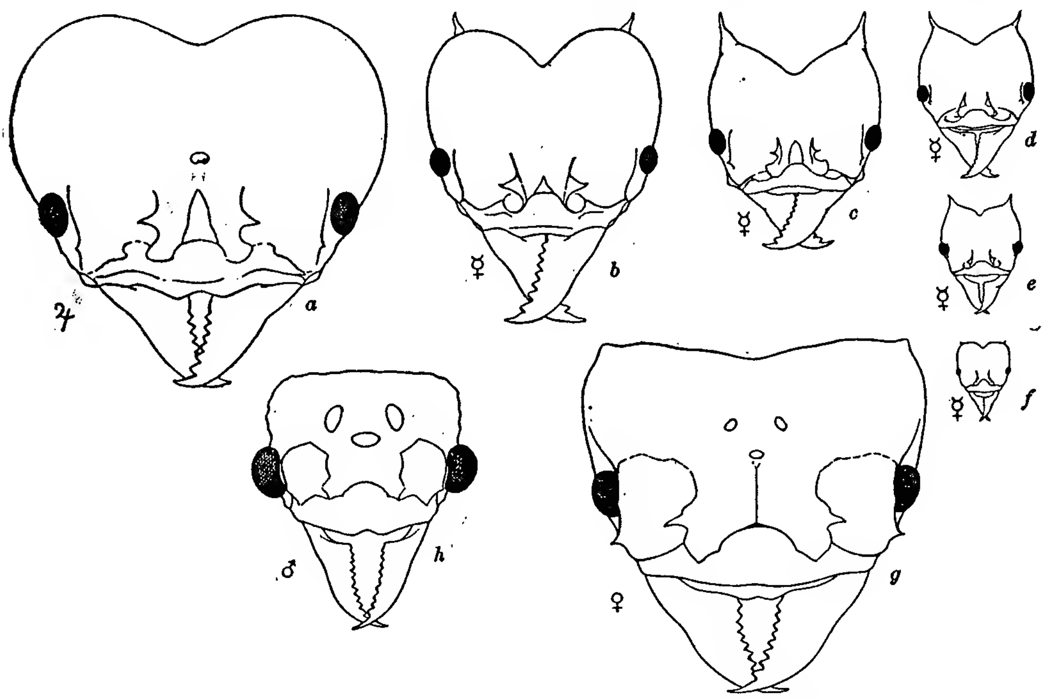

Fig. 11. Heads of the Various Castes of a Large Leaf-cutting Ant, *Atta cephalotes* L. from the Neotropical Region

a, soldier; *b* to *f*, series of workers from the major to the minima; *g*, female; *h*, male. The strong mandibles in all the forms are correlated with prominent occipital lobes or angles.

below (*g*) is the deälated fertile female, or queen, the small winged individual (*h*) is the male; the very large-headed individual (*a*) is the largest type of worker, or soldier, the very small individual (*f*) the worker proper. Between these two extremes we find in any flourishing colony of the species, a complete graded series of intermediates, some of which (*b* to *e*) are represented. The worker (*f*) forages worker, which has a very small, rounded rectangular head, as broad as long. The crushing mandibles gradually become mandibles of the biting type as we pass from the soldier to the worker proper, and in my preparations the flexor muscles, which in all the forms fill out nearly the whole cranium, show a corresponding gradual decrease in volume.

The same phenomenon is exhibited in

the Indomalayan harvester, *Pheidologeton diversus* (fig. 10), but in an even more exaggerated form. In this figure only the outlines of the heads of a series of soldier and worker individuals and of the queen and male are represented. In the soldier provision is made for the huge flexor muscles by such a great increase in the width as well as in the length of the head, that the difference between the two extremes of the worker series becomes enormous. The queen's head (*f*) resembles that of the soldier (*a*) but you will notice that the male (*g*), which has small mandibles, has a small, broad head, with very short and rounded occipital region.

Another instructive example is furnished by the large leaf-cutting and fungus-growing ants of the neotropical genus *Atta* (fig. 11). Among these the head of the biggest workers, or soldiers (*a*) is not only greatly enlarged but its front and occipital lobes are extremely convex. The leaves are cut by the intermediate worker castes (*b* to *e*) with the scissor-like mandibles, whereas the smallest workers (*f*) never leave the nest but live among the delicate hyphæ of the fungus-gardens, weeding out deleterious spores and alien mycelia. This caste, which therefore works only on soft materials, has small, weak mandibles and the head is accordingly very much smaller, narrower and less convex. The queen (*g*), which has to dig her nest in the soil and defend her young brood, has a head much like that of the larger workers. The male (*h*), unlike most male ants, has well-developed mandibles and therefore exhibits a much greater development of the head behind the eyes.

The series of worker ants which I have used for illustration recalls the graded series of Harvard professors who have been classified by some of the students as high high-brows, high-brows, low high-brows, high low-brows, low-brows and low low-brows. Some authors regard the soldiers, the highest high-brows of our ant series, as monstrous, or pathological forms on account of the excessive development of their crania. Certain facts might seem to lend support to such an opinion. If the soldier of *Ph. instabilis* be placed on its head on a perfectly smooth, hard, horizontal surface, the insect may be quite unable to right itself and may even die standing on its head. But this is a typical laboratory experiment. In its natural environment the soldier never encounters such surfaces. Closer study shows that all these sup-

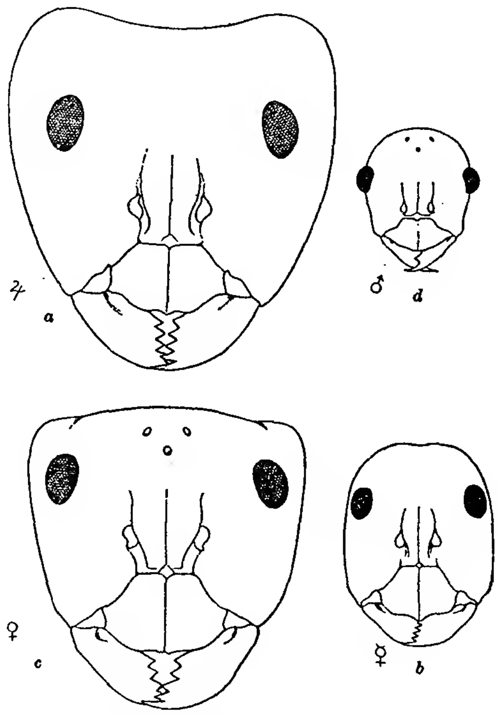

Fig. 12. Heads of Four Castes of an Australian Formicine Ant, *Camponotus (Myrmosaulus) bellicosus* Forel

a, worker maxima; *b*, worker minima; *c*, female; *d*, male. Note prominence of occipital corners in *a* and *c* with large mandibles and rounding of occiput in *b* and *d* with feeble mandibles.

posedly monstrous forms are really exquisitely specialized and adapted for the functions they have to perform in the life of their respective colonies. The soldiers of the harvesting *Pheidoles* and *Pheidologetons* are needed not only as seed-crushers, but those of the latter genus have another very different function. Several observers have seen groups of the minute *Pheidologeton* workers sitting quietly on the huge heads of the soldiers and riding to and from the nest. The soldiers of the insect-eating *Pheidoles* dismember the tough prey before or after it has been carried into the nest. Hingston (1922, p. 61 et seq.) has recently

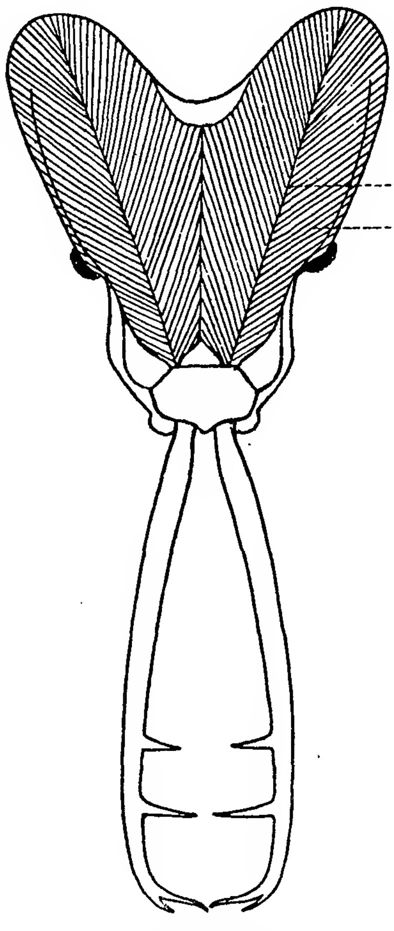

FIG. 13. HEAD OF *Strumigenys* SP., WORKER, SHOWING THE LONG GRAPPLING MANDIBLES, WITH THEIR FLEXOR MUSCLE FIBRES (*fl. m.*), AND THE PINNATE ATTACHMENT OF THE LATTER TO THE TENDONS (*t.*)

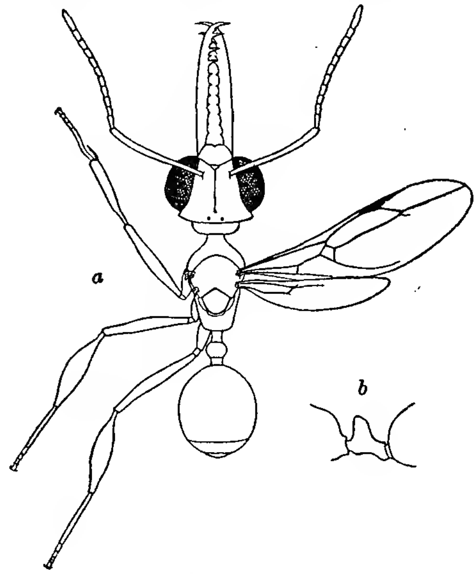

FIG. 14. *Myrmoteras donisthorpei* WHEELER, A FORMICINE ANT FROM BORNEO

a, female; *b*, petiole. Note the grappling mandibles and huge eyes

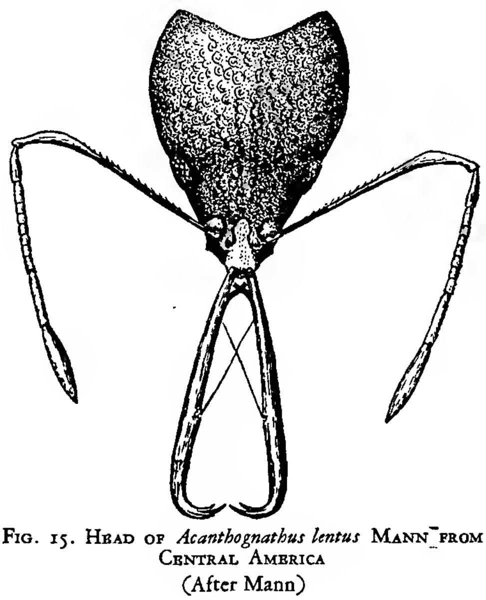

FIG. 15. HEAD OF *Acanthognathus lentus* MANN FROM CENTRAL AMERICA

(After Mann)

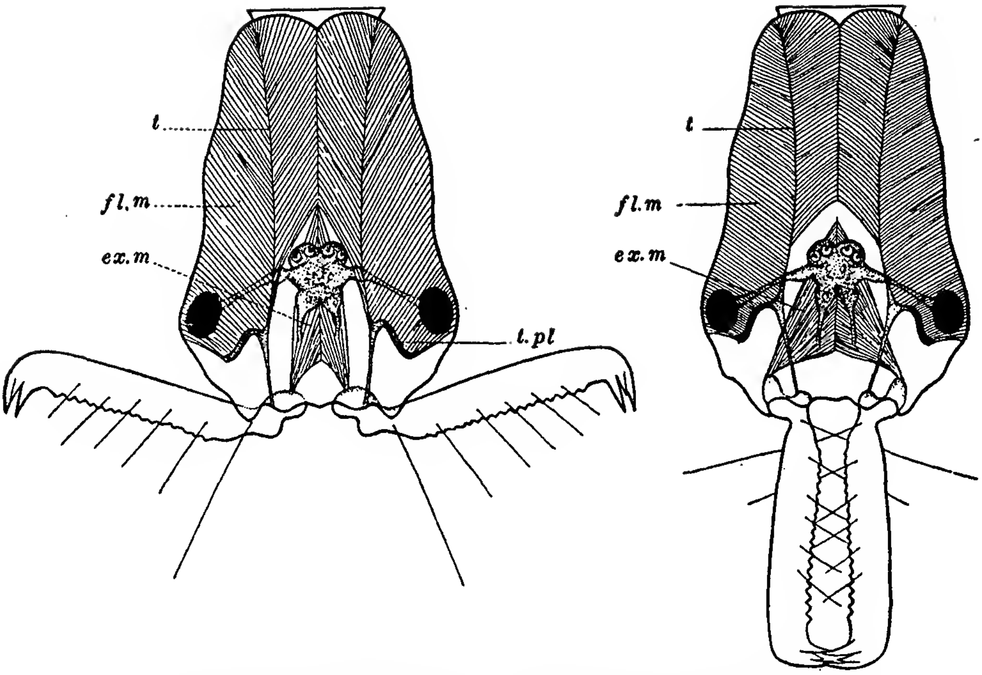

FIG. 16. HEAD OF *Odontomachus vastatus* F. WITH MANDIBLES OPEN AND CLOSED

ex. m., extensor muscles of mandibles; *fl. m.*, flexor muscles of latter; *t.*, tendon; *t. pl.*, plate of tendon

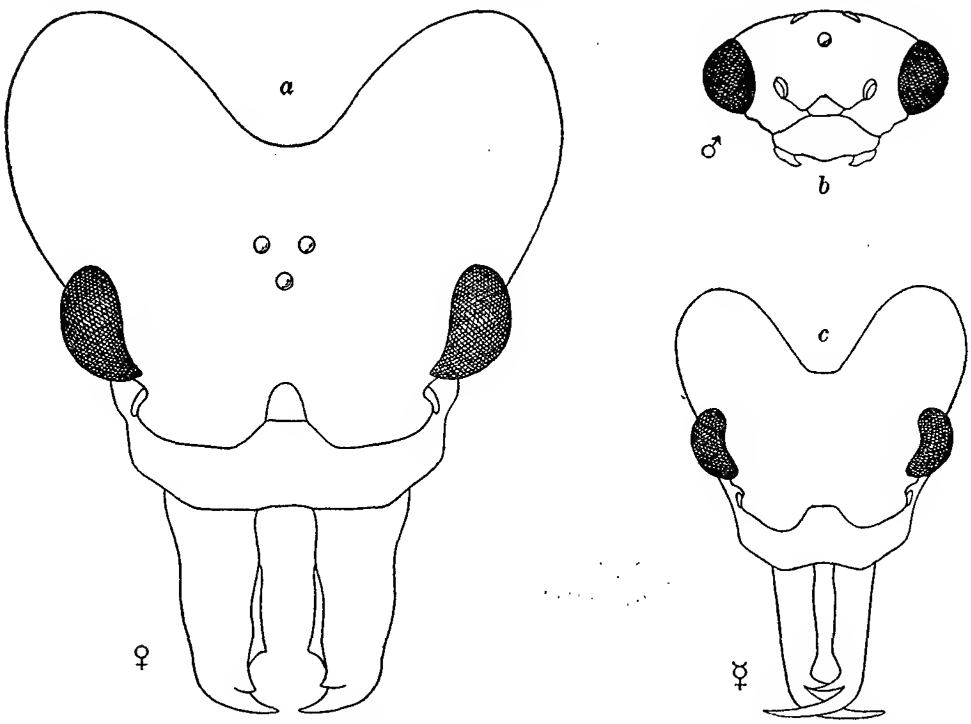

FIG. 17. HEADS OF SOUTH AMERICAN ANT, *Daceton armigerum* PERTY, WITH CLIPPING MANDIBLES

a, head of female; *b*, of male; *c*, of worker. Note the absence of occipital development correlated with vestigial mandibles in the male.

described in vivid language the extraordinary powers of communication exhibited by the diminutive *Pheidole indica* worker when notifying the soldiers to come out of the nest and oversee the transportation of the prey. As I have noticed a somewhat similar behavior in some of our American *Pheidoles* in the Southwestern States, I will quote part of his remarks:

As soon as a worker discovers a caterpillar or other suitable material for food, it proceeds to make a careful examination of its prey. It runs all over the caterpillar exploring it with its sensitive antennæ, shaking it with its jaws and attempting to drag it to the nest. The worker, satisfying itself that the discovery is suitable for storage and finding the removal of it beyond its own weak efforts, hastens off to the nest in great excitement and by the shortest route. It meets another worker on its path; their antennæ meet; the second worker is imbued with the enthusiasm of the first, has received information of the discovery and hastens off to the insect. A third, a fourth, and possibly more workers are similarly informed on the route and all hurry away to lend their assistance. But the excited discoverer hastens on to the nest. Now it has reached the entrance. It enters and is lost to view. In a few seconds a swarm of rushing, bustling and excited ants, come dashing headlong from the nest. From the way they are all lying in readiness just within the door and emerge at the same moment in one body as though they were awaiting a call for aid, I have no doubt but that these ants so divide their labor that certain workers are detailed for the duty of discovering food, and others, under the guidance of the soldiers, are under orders to remain in permanent readiness within the door of the nest to hurry out and render assistance when news arrives that a discovery has been made.

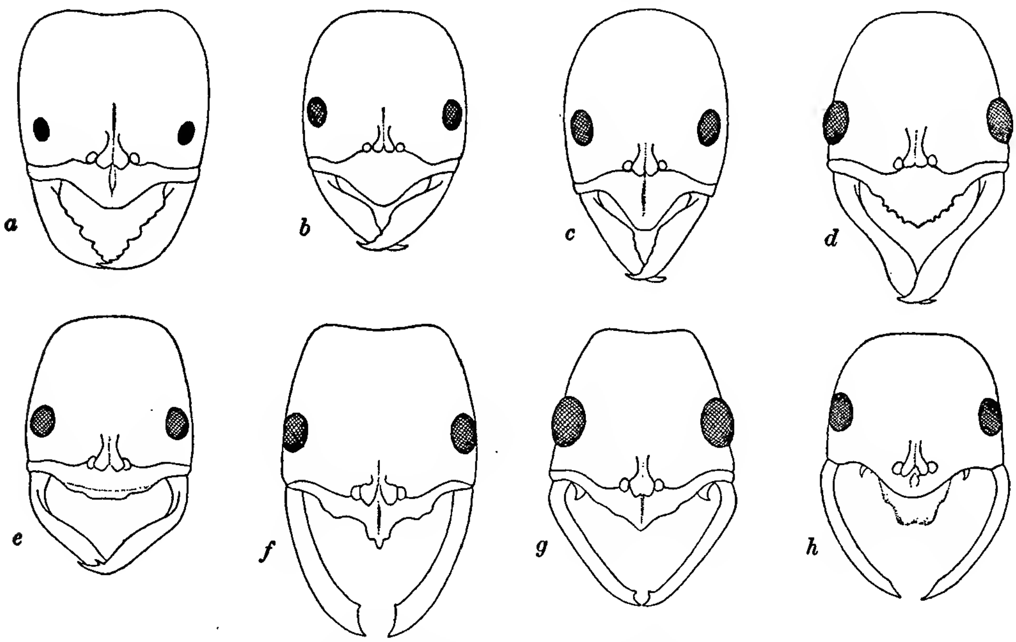

Fig. 18. Heads of Eight Species of *Leptogenys* (Subgenera *Leptogenys*, *Lobopelta*, *Odontoponera*, and *Machærogenys*), Showing Correlation of Feeble Mandibular Development with Narrowing and Rounding of Occipital Region of Head

The news has come. Out they swarm in a dense throng preceded by the soldiers. Without the slightest hesitation they hurry over the ground, passing and repassing one another in their excited haste. . . . . On all sides they besiege the larva, which tries in vain by violent contractions to throw off its enemies. The battle grows hot and fierce. The caterpillar in its struggles now gains the mastery, but ants hurrying on in increasing numbers gradually overpower it. Workers, at intervals, retire from the battle and hasten back to the nest at the greatest speed to call out more reinforcements and hurl them into the

fight. The caterpillar weakens; it cannot face these repeated additions to the strength of its foes. It is overwhelmed by the force of numbers, soon becomes exhausted, and then lies at the mercy of the ants which, clinging in a body round their powerless victim, drag it slowly to the nest.

Hingston also describes the peculiar behavior of the soldiers during migration to a new nest.

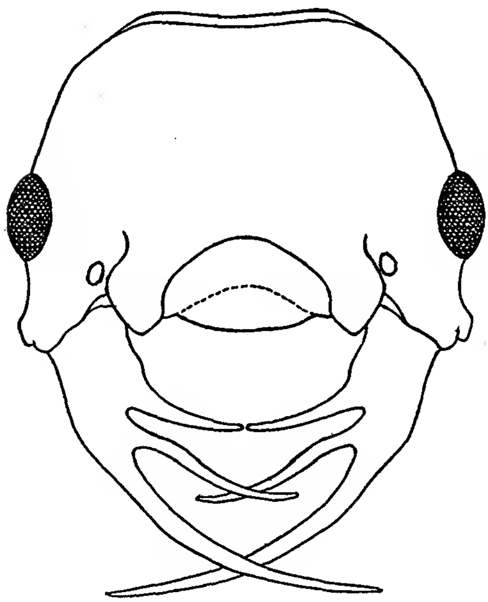

FIG. 19. HEAD OF WORKER OF THE NEOTROPICAL *Thaumatomyrmex ferox* MANN, WITH WEAK, ABERRANT, THREE-TOOTHED MANDIBLES AND UNDERDEVELOPED OCCIPITAL REGION

The main burden of toil falls on the smaller workers. It is they alone that transport the larvæ, and they often carry their companions from nest to nest. The soldiers carry nothing. They are not humble toilers, but are the directors of the transport. They are the aristocracy of ant life. They hurry out of the nest singly and at intervals with a throng of laden ants following in their rear, and as each powerful soldier hastens along the migrating line it looks like an officer leading and directing his company of men. Nor do the soldiers return again to the old nest. The smaller workers, once they have deposited their larvæ in the new nest, hasten back for a fresh burden, but a returning soldier is never seen. It, no doubt, busies itself with important duties within the new nest, but takes no further part in the migrating line.

It may be readily shown that the conditions sketched for the cranial physiognomy of ants obtain also in other groups of insects, and especially among the Coleoptera. Two examples must suffice. Among many Lucanidæ, or stag-beetles (fig. 22) we find series of forms closely analogous to those of *Pheidole*, *Pheidologeton* and *Atta*, but in the beetles it is the males that are polymorphic. They

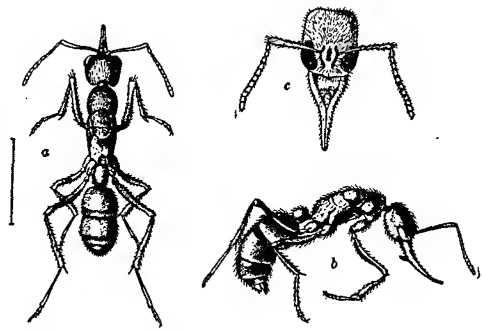

FIG. 20. A JUMPING PONERINE ANT, *Harpegnathos venator* VAR. *rugosus* WITH ABERRANT MANDIBLES, FROM HONGKONG

a, deälated female, dorsal view; *b*, same, lateral view; *c*, head, from above. (After G. May.)

have been arranged according to the development of the mandibles in series beginning with large macrodont forms, passing through amphiodont, eopriodont and priodont forms and ending with individuals with small mandibles like the female (Griffini, 1905, Champy, 1924). In such a series the head gradually decreases in width *pari passu* with a reduction in the size of the mandibles. There is also a corresponding reduction in the volume of the prothorax and fore legs. This occurs also in the ant series and might be expected, because the muscles that raise, lower and rotate the head are situated in the prothorax. In the highest highbrows among the Lucanids we even find the posterior corners of the head pro-

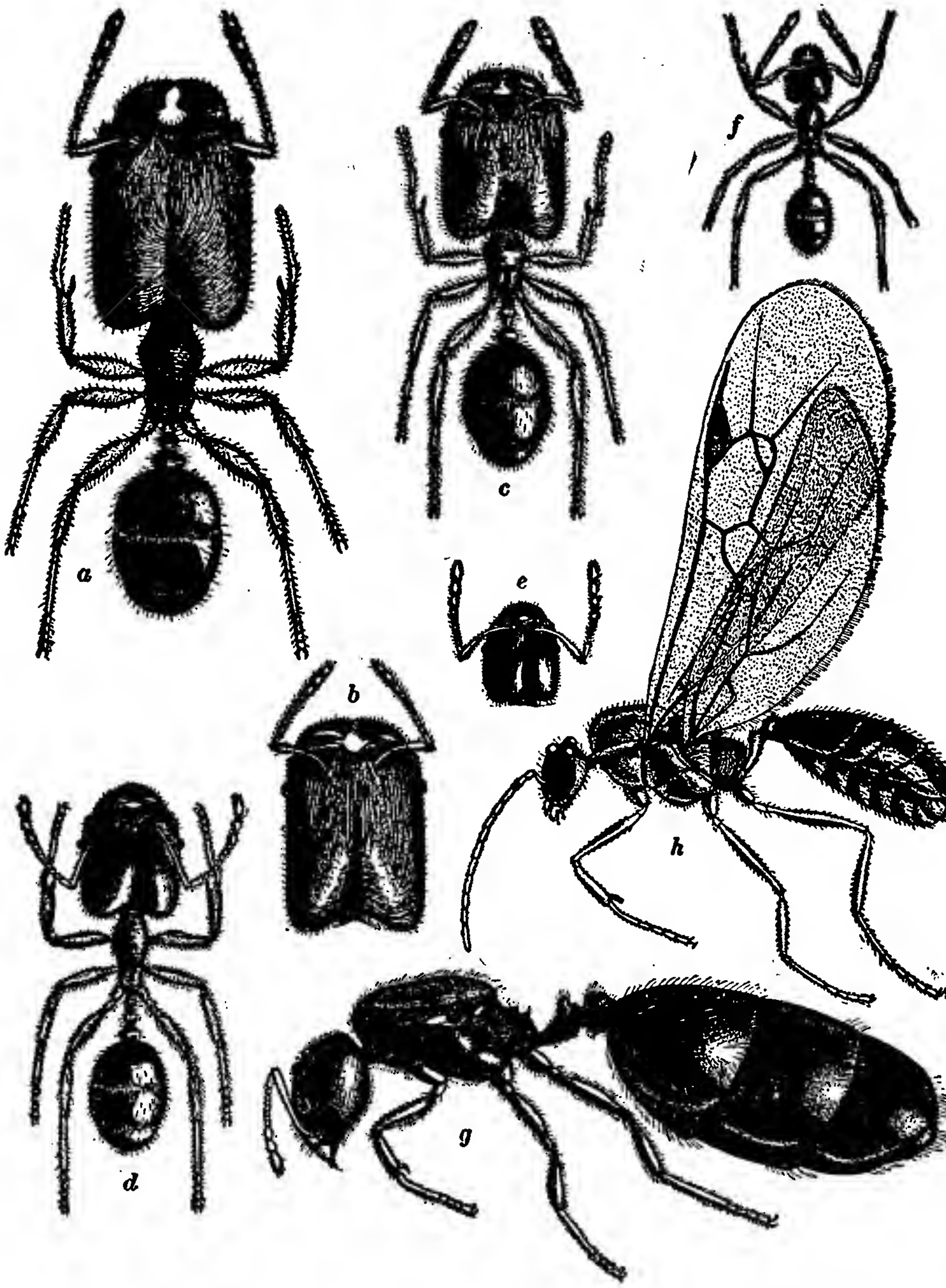

FIG. 21. VARIOUS PHASES OF A SMALL HARVESTING ANT, *Pheidole instabilis*, FROM TEXAS

a, soldier; *f*, worker; *b–e*, forms intermediate between soldier and worker; *g*, female (deälated); *h*, male. All the figures are drawn to the same scale.

vided with crests or protuberances which increase the surface for the insertion of the enormous mandibular flexors and are therefore analogous to the bony crests on the skulls of many mammals that have powerful jaws and temporal muscles.

The correlation between the size and shape of the mandibles, head and pro-

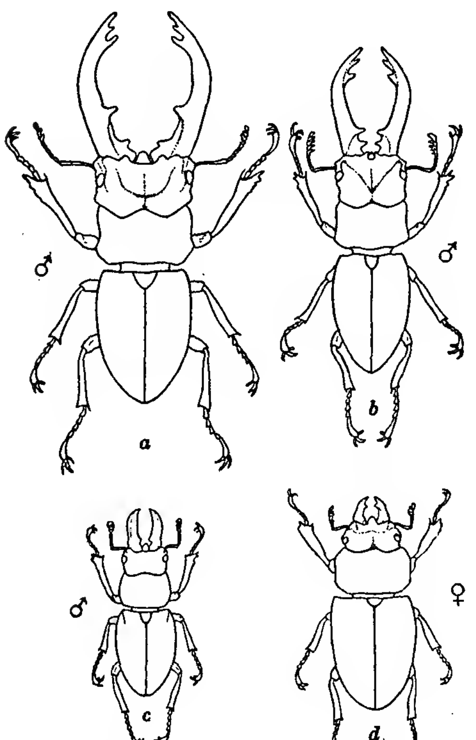

FIG. 22. FORMS OF A LUCANID BEETLE, *Metapodontus umbangi* FAIRM

a, heteromorphic male; *b*, intermediate male; *c*, homœomorphic male; *d*, female. (After Planet.)

thorax is also clearly shown by a comparison of the male and female *Eupsalis minuta* (fig. 23). In the specimens figured, whose bodies behind the prothorax happen to be of the same size, you will observe that the prothorax is shorter and anteriorly narrowed in the female in correlation with the much smaller head and mandibles. The slender prolongation of the head in this sex is specially adapted for oviposition. The huge mandibles are used by the male Lucanids in their fierce sexual contests, which have been witnessed by many observers. The males of Eupsalis also fight with their mandibles, though according to Leconte and Horn (1876) their combats are bloodless and "seem, so far as the records go, to be actuated rather by

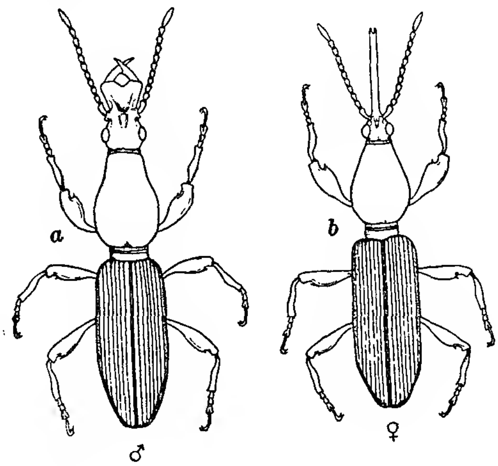

FIG. 23. A NORTH AMERICAN BRENTHID BEETLE, *Eupsalis minuta* DRURY

a, male; *b*, female

chivalric sentiment, than by animal passion." According to Blatchley and Long (1916, p. 21):

> Smith says that when the beaks of the females become wedged, as they sometimes do, the males use their forceps-like jaws to pull them out, but Riley states that the male helps in removing the beak by "stationing himself at a right angle with her body and pressing his heavy prosternum against the tip of her abdomen, her stout fore legs thus serving as a fulcrum and her long body as a lever."

After this digression I return to a consideration of some other types of heads and mandibles among the ants. Even in the smallest workers of the species hitherto described the mandibles are moderately strong and of the typical biting type, but in species that feed on

soft substances and excavate their nests in soft soil or very rotten wood or merely occupy cavities made by other insects, the mandibles may be weak and narrow and the head not only elongate and rounded behind but drawn out into a distinct neck. Among the best examples

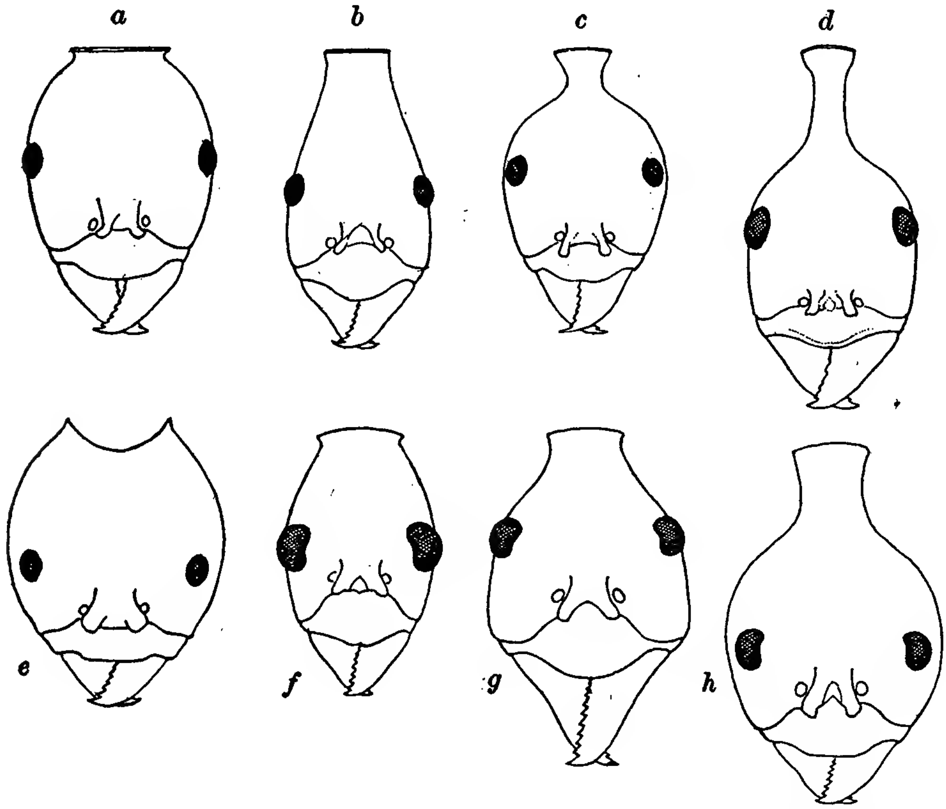

FIG. 24. PARALLEL DEVELOPMENT IN THE CONTRACTION OF THE OCCIPITAL REGION IN OLD WORLD SPECIES OF *Aphaenogaster* (*a–d*) AND NEOTROPICAL SPECIES OF *Dolichoderus* (*e–h*)

a, *Aphaenogaster* (*Nystalomyrma*) *longiceps* Sm. (Australia); *b*, *A.* (*Deromyrma*) *phillipsi* Wheeler and Mann (Palestine); *c*, *A.* (*Deromyrma*) *swammerdami* Forel (Madagascar); *d*, *A.* (*Planimyrma*) *loriai* Emery (New Guinea); *e*, *Dolichoderus decollatus* Sm.; *f*, *D. imitator* Emery; *g*, *D. rugosus* Sm.; *h*, *D. attelaboides* Fabr.

of this condition is *Apterostigma pilosum*. This ant, though related to *Atta*, does not nest in coarse ground and cut leaves but lives in cavities under bark or stones and makes its fungus gardens of insect excrement. Similar types of head (fig. 24*c*, *d*, *h*) occur in other asthenic species belonging to very different genera (*Aphaenogaster*, *Dolichoderus*, *Leptogenys*, *Leptomyrmex*) either as the only type among the workers or in the worker minima of species which have a large-headed soldier or worker maxima (*Dinomyrmex*, *Pheidole*, *Ischnomyrmex*).

The grappling and piercing mandibles are also comparatively weak organs. The former, which are well-developed in certain Ponerinæ like the "bull-dog" ants of Australia and the species of the peculiar genus *Mystrium* are adapted for holding onto the prey while the abdomen is being bent around and the powerful sting inserted. Large hook-like mandibles

which seem to combine the functions of grappling and piercing organs are found in the soldiers of some of the army ants (*Eciton sens. str.*) (fig. 25*a*) although the next lower grade of worker (*b*) has curved, grappling mandibles and the smaller and far more abundant worker forms have cutting or biting mandibles (*c*, *d*). Both in our slave-making "amazons" of the genus *Polyergus* and in certain other genera (*Strongylognathus* and *Leptogenys*) the mandibles are of the true piercing type. The amazons use them for perforating the heads of their enemies and the species of *Leptogenys* (fig. 18*d–h*) evidently kill the soft-bodied termites, on which they prey, in the same manner. It will be noticed that the posterior portion of the head is distinctly narrowed and rounded in these various forms.

A highly specialized condition obtains in the clipping mandibles which show some extraordinary convergent developments in genera belonging to three different subfamilies of ants (the Odontomachii (fig. 16) among the Ponerinæ, the Dacetonini among the Myrmicinæ (fig. 17) and the Myrmoterini among the Formicinæ (fig. 14)). *Odontomachus* may be selected for more detailed description (fig. 16). The numerous species, known as clicking ants ("fourmis tic") in the tropics, have singular, elongate-subhexagonal heads, with the eyes placed far forward on lateral eminences while the mandibles are inserted close together at the anterior end of the head and consist of long, parallel-sided blades, with a few powerful, abruptly inflected terminal teeth and on their inner border a series of serrate denticles and long sense-hairs. The insect has a curious method of employing these organs. When it is excited they are widely opened as in the figure, and as soon as the long hairs, which act as triggers, touch an object, the blades are closed with lightning rapidity and an audible click. If during the closure their tips happen to strike against a hard body the insect is thrown off its feet and backward through the air to a distance of several inches. On opening an *Odontomachus* nest on a hot day one may hear a series of sharp clicks and find that the whole colony has suddenly evaporated into the surrounding vegetation. When the worker is hunting it cautiously ap-

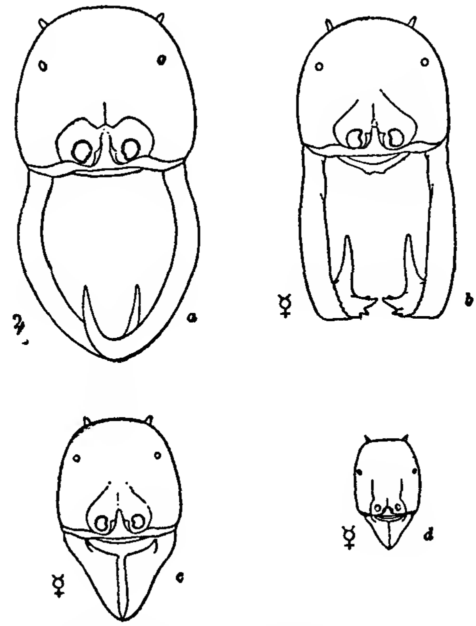

FIG. 25. HEADS OF A NEOTROPICAL ARMY OR LEGIONARY ANT (*Eciton burchelli* WESTW.)
a, soldier; *b*, form intermediate between soldier and worker; *c*, large, *d*, small worker.

proaches its insect prey with wide-open mandibles, suddenly darts forward, clips off an appendage and then retreats. It again advances and clips off another leg, antenna or wing and keeps repeating the performance till it has reduced its prey to a helpless, easily mastered torso. [For additional notes on the habits of Odontomachus see Wheeler (1900).]

In conformity with this unique behavior, the musculature of the mandibles

is peculiarly modified. The flexor mandibulæ (*fl.m.*) is very long and fills out the whole elongated posterior portion of the cranium. The tendon (*t*), attached to the swollen internal mandibular hinge, is expanded behind near the eye into a twisted, somewhat crescentic, chitinous plate (*t.pl.*) from which two long slender tendons run back very nearly to the posterior border of the head. Only one of these tendons is shown in the figure, because the other, which runs mesially and ventrally is concealed. The muscle-fibres are numerous, very short and attached to the tendons like the barbs of a feather to

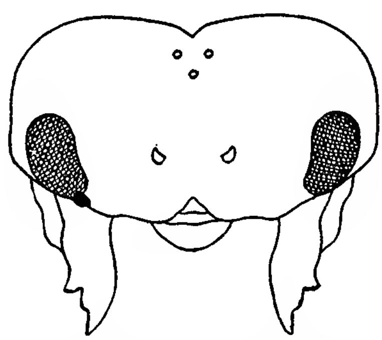

Fig. 26. Head of *Alysia manducator* Panz. of Europe
Note the great width of the head, presumably to accommodate the *extensor* muscles of the mandibles, and the teeth on the *external* borders of the latter.

its shaft, but in three dimensions of space. In the neighborhood of the eye fibres also run from the crescentic chitinous plate to the anterolateral walls of the cranium. Since short muscle-fibres can contract more quickly than long ones, the whole arrangement seems to be beautifully suited to closing the jaws with much greater velocity than in other ants. And the large size of the flexor muscle as a whole shows that closure is effected with considerable vigor.

The mandibles of Dacetonine ants show a bewildering variety of forms, often much like those of *Odontomachus*. Some of the species are also able to leap backward. The head, however, has a very different shape (figs. 13 and 15). It is usually more or less cordate in the worker and female, with very prominent occipital lobes and these are filled with the huge flexor mandibulæ muscles. Their fibres, in some of the species at least, are arranged along the sides of a long tendon (fig. 13). Unfortunately we possess no information in regard to the feeding habits of these ants. If we may judge from their faces they certainly do not spend their lives diffusing sweetness and light. The heads of the male Dacetonini are extraordinarily different, as will be seen from the figure of the South American *Daceton armigerum* (fig. 17). The two large drawings (*a* and *c*) represent the heads of the female and worker, the small one the head of the male (*b*). Notice the vestigial condition of the mandibles, the shortness of the cranium and the complete suppression of the great lobes which in the other castes contain the flexor muscles of the mandibles. Owing to these deficiencies the countenance of the male wears a very meek and vacuous expression compared with the satanic countenances of the female phases.

Among the ants with aberrant types of mandibles I will select only two. In one of them, *Thaumatomyrmex* (fig. 19), of which only a couple of tropical American species are known, each mandible is split into three long slender spines. The narrowing and rounding of the posterior portion of the head indicates that the flexor muscles must be very feeble. We know nothing of the habits of these insects, only a few, isolated specimens of which have ever been taken. Perhaps they feed on very soft-bodied larvæ or small snails in which case the mandibles might be used for puncturing the integument of the prey in several places. The other type is that of *Harpegnathos*, an

East Indian ant with extraordinary mandibles known to be employed in leaping (fig. 20). The insect apparently bends its head completely under the body, presses the tips of the mandibles against the ground and by suddenly raising its head, leaps forward to a distance of a yard or more. This habit, however, does not completely account for the unusual conformation of the mandibular blades, especially of their large basal teeth (Wheeler, 1922).

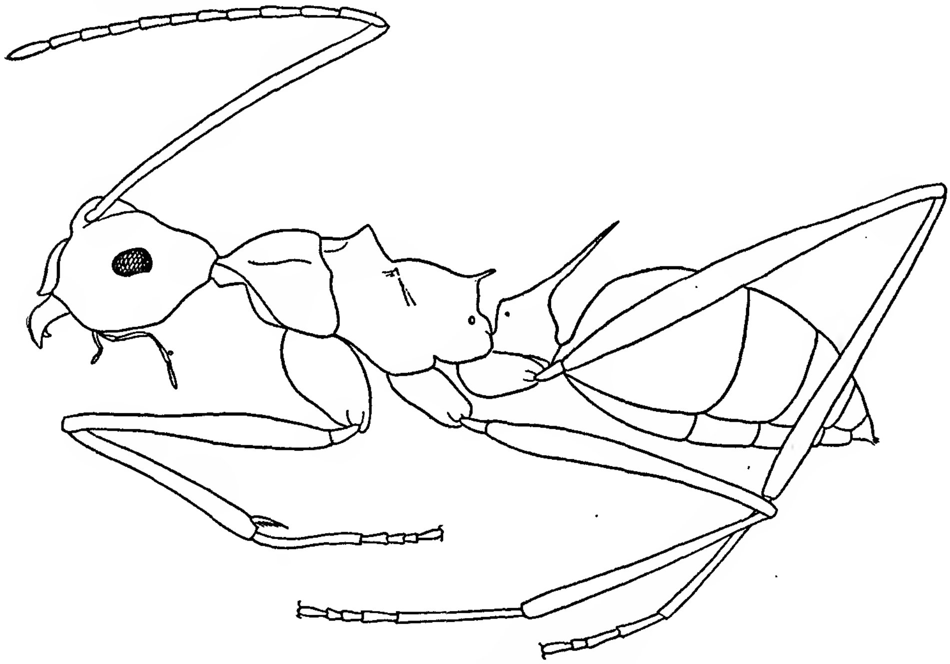

FIG. 27. *Polyrhachis (Myrmatopa) ulysses* FOREL FROM THE SOLOMON ISLANDS; WORKER IN PROFILE, SHOWING CONVEXITY OF THE FRONT

Much of what I have said about the mandibles of ants, their musculature and the shape of the head will, I believe, hold good of many other mandibulate insects. Professor C. T. Brues, however, calls my attention to two unrelated groups of Parasitic Hymenoptera, the Alysiidæ and Vanhorniidæ, in which the function of the mandibles and probably also the development of their musculature are reversed. In the accompanying outline figure of the head of *Alysia manducator* (fig. 26) it will be observed that the mandibles have the teeth on their external instead of their internal borders. Obviously in this case the extensor muscles have much more work to perform than the flexors and are therefore probably larger. This is indicated by the unusual width of the head and the distance between the eyes. Of course, such exodont mandibles cannot be used for biting or mastication, but might be employed by the insect in forcing its way through soft wood, mushroom-tissues, etc. We unfortunately possess no observations on the habits of the Alysiidæ beyond the fact that their larvæ live in the larvæ of various Diptera, Coleoptera and Lepidoptera.

The heads of ants vary considerably in the convexity of their dorsal surface. As a rule, they are most convex in the region

of the vertex and occiput, a condition which is, of course, correlated with the development of the flexores mandibulæ already described, but in a few genera and notably in *Polyrhachis* (fig. 27) the front is conspicuously convex or protuberant. Since the antennæ are always long and very mobile in such insects I believe that the frontal convexity must be due to the greater development of the flexor and extensor antennal muscles, which run from the articulations of the appendages downward, backward and outward and are inserted on the limbs of the tentorium. I advance this merely as a suggestion, because I have not yet had an opportunity to study the anatomy of *Polyrhachis*.

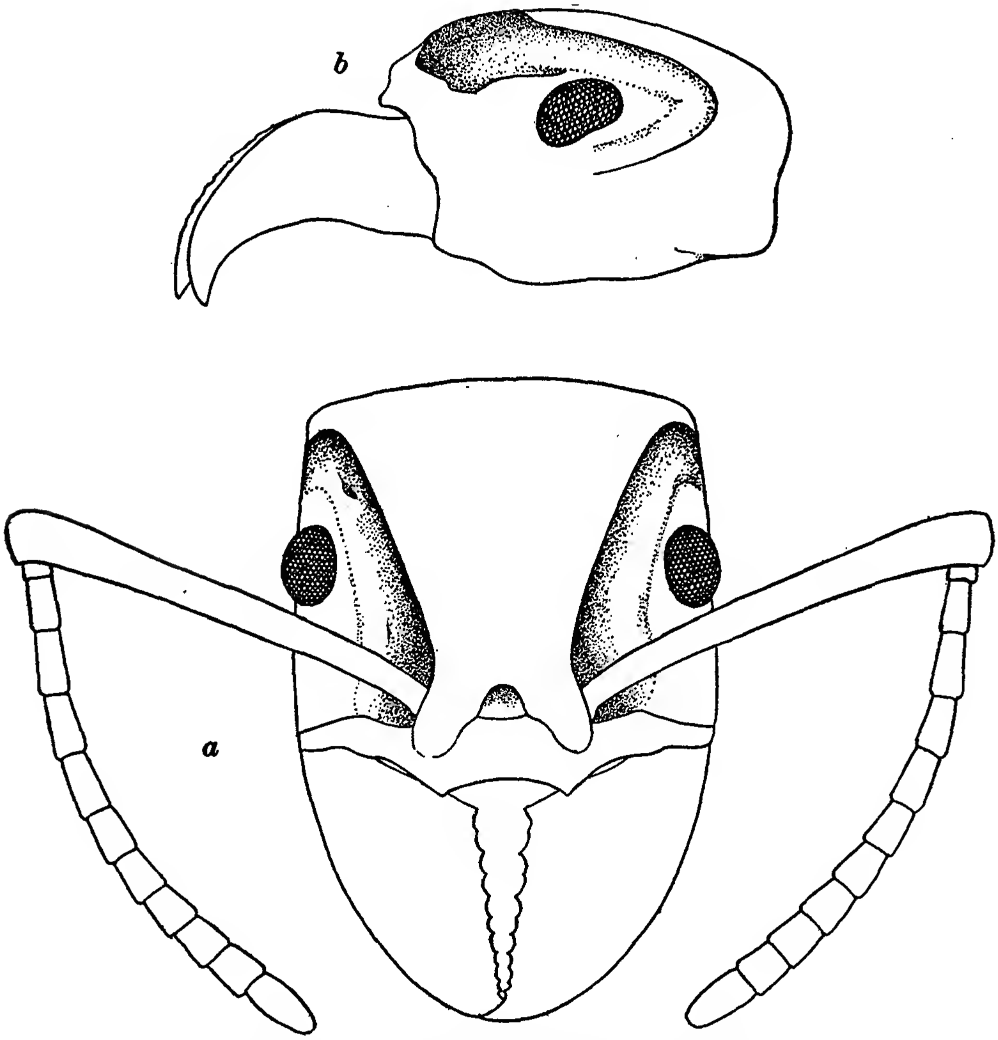

Fig. 28. Head of the Formidable "Tucandeira" Ant, *Paraponera clavata* Fabr., of Tropical America, Showing the Peculiar Angulate Scrobe
a, seen from above; *b*, in profile

DEVELOPMENT OF GROOVES FOR ANTENNÆ

The sides of the head in ants are sometimes peculiarly modified by the development of grooves, or scrobes for the partial or complete concealment of the antennæ. In their simplest form, e.g. in many species of *Pheidole*, *Harpagoxenus* and *Tetramorium*, these scrobes are formed by a backward prolongation of the frontal carinæ and a longitudinal depression of the adjacent cranial surfaces. In certain other genera, however, the grooves become deeper. In *Paraponera* (fig. 28) we find a very peculiar scrobe with two limbs forming an angle around the eye. At first sight this structure would seem to be an adaptation for receiving both the scape and the flagellum of the antenna, but the scape and flagellum are really too long to form an angle that will fit into the scrobe. Hence the dorsal limb can accommodate only the basal portion of the scape when it is folded back and the ventral limb only the tip of the flagellum. In *Paranomopone* the scrobe is divided near the middle by a slender partition into two grooves one of which accommodates the scape, the other the flagellum. In still other genera the scrobe is simple but sufficiently deep to receive the whole folded antenna or at any rate the whole scape (fig. 29). In *Cryptocerus* (*a*) the scrobe lies in front of the eye, in *Procryptocerus* and *Meranoplus* (*b* and *c*) it runs backward over the eye, in *Cataulacus* (*d*) it descends below the eye. In all of these genera, and especially in *Cryptocerus*, the frontal carinæ may be greatly expanded laterally, so that the head becomes very broad and shield-shaped, with plate-like lateral margins (fig. 30).

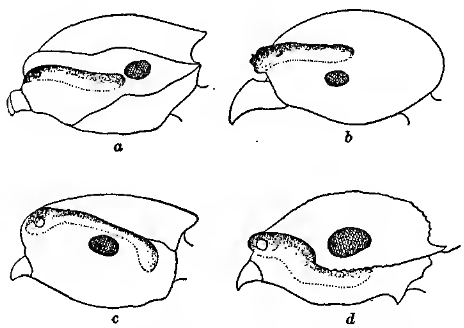

FIG. 29. PROFILES OF HEADS OF VARIOUS ANTS TO SHOW DEVELOPMENT OF THE ANTENNAL SCROBE AND ITS RELATION TO THE EYE

a, *Cryptocerus multispinus* Sm.; *b*, *Meranoplus mars* Forel; *c*, *Procryptocerus belti* Forel; *d*, *Cataulacus erinaceus* Stitz

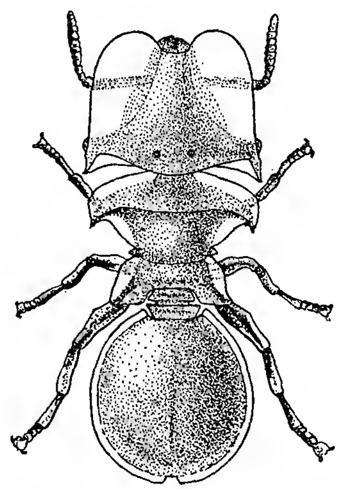

FIG. 30. *Cryptocerus* (*Zacryptocerus*) *clypeatus* F.; WORKER, WITH THE HEAD BROADENED AND FLATTENED FOR USE IN PHRAGMOSIS

(After C. Emery)

The scrobes suggest an interesting evolutionary problem. It would seem that they might be formed in the pupa by the pressure of the antennæ against the still soft and plastic cranial integument, but when we examine the young pupæ of the various genera I have mentioned, we find that the antennæ are not folded up against the sides of the head but are drawn down over the ventral surface of the legs as in the pupæ of many other insects. The scrobes therefore develop independently during the ontogeny and we are compelled to conclude that

these grooves, so beautifully adapted in the adult to the reception and protection of the very sensitive and important antennæ, must have arisen during the phylogeny of the various species in which they occur. The notion that they were produced by natural selection may be dismissed as improbable for the simple reason that they cannot have had survival value, because they are altogether lacking in most of the larger and more dominant genera (*Monomorium*, *Crematogaster*, *Polyrhachis*, *Formica*, most *Camponotus*, etc.). The only hypotheses, it seems to me, that might be advanced to account for the scrobes are those that have been discussed in connection with many similar cases of functionally correlated structures, namely, first, the Lamarckian hypothesis that habitual pressure of the antennæ against the hard integument of the adult cranium has affected the germplasm in such a manner as to lead to the gradual development of scrobes in the pupal offspring of succeeding generations, and second, the mutation hypothesis of the chance, spontaneous origin of scrobe-producing genes in the germplasm. The latter hypothesis fails to account for the highly adaptive character of the scrobes and the former labors, of course, under the difficulty of explaining how the habitual pressure of the antennæ against the hard, unyielding cranial cuticula of the adult could translate itself into a definite formative, or morphogenic tendency in the individuals of succeeding generations.

PROBLEMS OF ADAPTATION

A number of exquisite structures similar to those here described have been discussed by Cuénot (1925) in his very interesting little book on adaptation under the head of "coaptations." These he defines as "reciprocal adjustments of two independent parts analogous to that formed by the blade fitting into the handle-groove of a pocket-knife, or a button into its button-hole." As examples he cites the fore legs of certain Phasmids which are curiously bent at the bases of the femora to fit around the head, a case originally described by Stockard (1909), the pressure-button (used on gloves and invented in France about 1886), shown in the two attachments of the mantle in cuttle-fishes and the attachment of the hemielytra to the thorax in numerous aquatic Hemiptera, or Hydrocorisa (*Ranatra*, *Belostoma*, *Notonecta*, *Naucoris*, etc.), the devices in many insects for attaching or fitting the wings or elytra to one another, the coaptation of the blades of the ovipositor in Orthoptera, the stridulatory apparatus of Elaterids and other insects and the raptorial fore legs of numerous bugs, Mantids, Mantispids, scorpions and crustaceans. To this list we may add the Hymenopteran strigil which is formed by the spur of the tibia and basitarsus. After excluding the origin of such structures by mutation, and omitting all mention of the Lamarckian hypothesis, Cuénot says:

> Without a doubt, coaptation is the end-stage of a *directed* evolution. Sufficient indications of this evolution are known to permit its affirmation. There are Phasganourids with short ovipositors which have gutters that are rather imperfect though adequate fot the movements of oviposition. There are, foreshadowing the saltatory apparatus of Elaterids, certain imperfect conformations of a similar type; the *Corisas* have an apparatus simpler and less compact than the pressure-button of other aquatic Hemiptera, many predatory insects have ambulatory legs which serve equally well for seizing the prey though not of the highly differentiated type of the specialized raptorial legs in the Mantids and Naucorids. Now the only directing agency we know is Darwinian selection. This would have to play the rôle of a handicraftsman gradually correcting and perfecting his work, successively and tentatively, till it attained a complete and definitive functional specialization which could not be surpassed. Even admitting the omnipotence of natural selection, however, it could

not create the coördinated details of the coaptations, and it is just the origin of these details we find so difficult to understand. And then how improbable it is that the elytral apparatus of a *Lucanus*, the spur of the raptorial legs of a *Ranatra*, the stridulatory rasp of a longicorn, can have had sufficient vital importance during their incipient stages to have brought about differential extinction! But after these negations, nothing remains. It would be pure metaphysical amusement to imagine within the species a meticulous and fanciful demon, a regulator and director of mutations, even if he were decorated, as he has been by some, with such pompous epithets as "internal perfective tendency," "élan vital," "entelechy," or some other term. Again we must resign ourselves to saying: *ignoramus!*

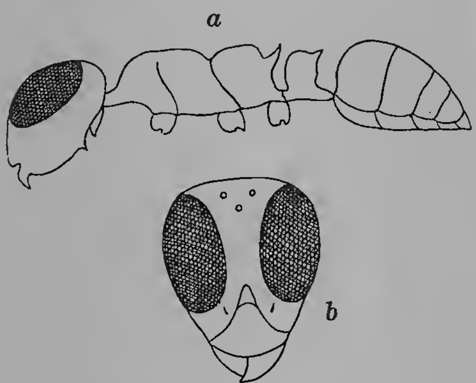

FIG. 31. *Santschiella kohli* FOREL; A HUGE-EYED FORMICINE ANT FROM THE CONGO

a, worker in profile; *b*, head of same from above. (After Forel.)

DEVELOPMENT OF EYES

Much might be said about the physiognomic significance of the eyes of ants and other insects, but the space allotted to this article and the reader's patience are limited, and I must be brief. In nearly all male Formicidæ, of course, the eyes are very large, but this is true of the females and workers only in a few rather primitive and archaic genera. The facial expression of these macrophthalmic forms is very unlike that of other ants. Thus *Santschiella* (fig. 31), which is known only from a single worker specimen taken in the Belgian Congo looks as if it were

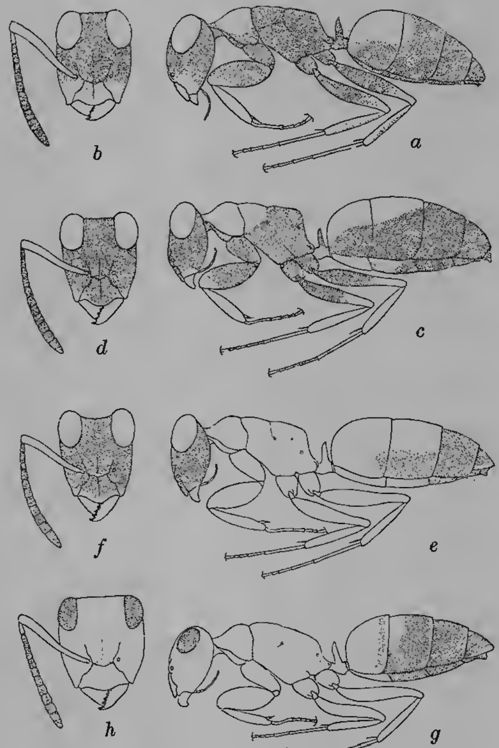

FIG. 32. WORKERS OF FOUR SPECIES OF THE LARGE-EYED AUSTRALIAN GENUS *Opisthopsis*

a and *b*, *O. respiciens* Sm.; *c* and *d*, *O. pictus* Emery var. *lepidus* Wheeler; *e* and *f*, *O. rufithorax* Emery; *g* and *h*, *O. major* Forel.

FIG. 33. A LARGE-EYED LEAPING ANT, *Gigantiops destructor* FROM BRITISH GUIANA

Dorsal and lateral view of worker and head seen from above.

hopelessly flabbergasted by the problem of existence and therefore resigned to race-suicide, and the species of the Australian genus *Opisthopsis* (fig. 32) and the neotropical *Gigantiops* (fig. 33), which have the large eyes at the posterior corners of the head, wear the expression of pained astonishment which as children we have all seen on the face of some school-marm or elderly maiden relative. It is more difficult to characterize the expression of the East Indian *Myrmoteras* (fig. 14) with its unique combination of huge eyes and clipping mandibles. If there are Anthony Comstocks, movie censors and prohibition agents among the ants we might, perhaps, expect them to have just such faces.

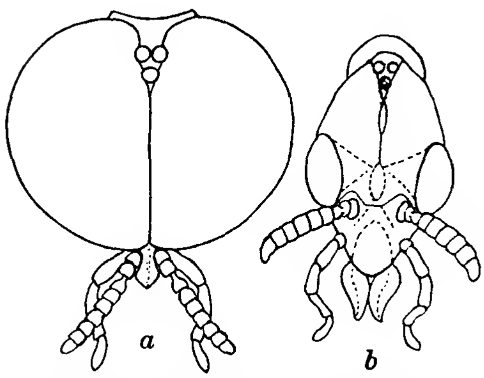

FIG. 34. *Bibio hortulanus* L., A EUROPEAN DIPTERON *a*, head of male; *b*, head of female. (After Berlese)

Large as are the eyes in these various ants they are not nearly as well-developed as those of many other insects, like the Diptera, Lepidoptera, Odonata, many Hemiptera, etc. In most of these orders, however, the mandibles are poorly developed or reduced to stylet-like appendages. In many male Diptera the eyes form nearly the whole head. An instructive case is furnished by *Bibio* (fig. 34) in which this condition is seen in the male, while the female has very small eyes and a very different head, narrowed and rounded behind like that of certain ants (*Lobopelta*) with poorly developed mandibles.

BEARDED ANTS

Of course, the physiognomy of ants is also determined to some extent by the character of the sculpture and pilosity. The sculpture, especially when it assumes the form of rugæ or reticulations is sometimes strangely suggestive of the wrinkles in the aged human countenance (*Diacamma*, some species of *Pheidole*, etc.). The various coiffures and styles of moustaches, whiskers and eyebrows are often extraordinary, but I will not dwell on them, because I might be tempted to depart too far from the arctic dignity so becoming to an entomologist. Nevertheless there is one type of beard to which I must call attention, because it has a very precise and practical function, unlike the human beard, which is supposed to have a great variety of functions—aesthetic, honorific, bacteriologic (or rather bacteriolegic), camouflagic, calorific, or merely problematic. And whereas in the human species it is the peculiar prerogative of the male to wear this form of pilosity, among the ants it is—*horribile dictu*—the females, i.e., the queens and workers that insist on cultivating it. But such improper customs prevail only among the species that live in deserts. Some years ago I discussed these ants in a tonsorial paper which might have attracted more attention had it been published in some barber's monthly instead of the Biological Bulletin (Wheeler, 1907).

Among the dominant ants of the arid, desert regions of the globe there are a number of species belonging to several genera and no less than three of the seven natural subfamilies (Myrmicinæ, Dolichoderinæ and Formicinæ) which have

series of conspicuously long, curved hairs on the chin (gula), mandibles, and clypeus (fig. 35). The arrangement of these hairs which form a kind of crate is most typical and most like that of the old-fashioned Irishman's chin-whiskers in the large Western harvesting ants of the genera *Pogonomyrmex* (fig. 35*a*) and *Veramessor*, and of the genus *Messor*, which ranges over the dryer parts of Africa,

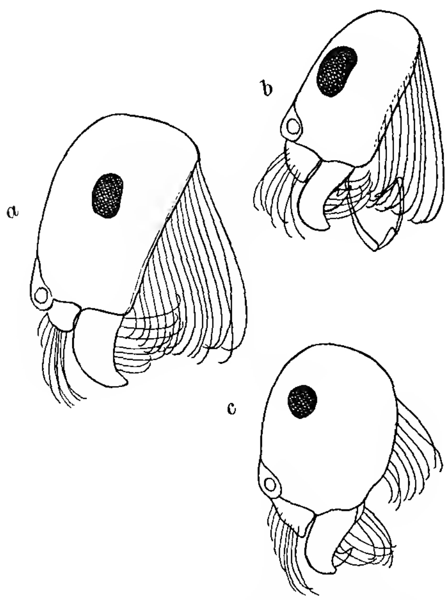

FIG. 35. HEADS OF DESERTICOLOUS ANTS IN PROFILE TO SHOW DEVELOPMENT OF THE PSAMMOPHORE IN THREE DIFFERENT SUBFAMILIES

a, *Pogonomyrmex californicus* from Southern California (Myrmicine); *b*, *Dorymyrmex* (*Psammomyrma*) *planidens* from Argentina (Dolichoderine); *c*, *Melophorus bagoti* from Central Australia (Formicine).

southern Europe, and Central Asia. Similar hairs are also developed in the deserticolous species of *Monomorium*, *Dorymyrmex* (fig. 35*b*), *Melophorus* (fig. 35*c*), *Cataglyphis*, *Myrmecocystus*, and *Camponotus*. Santschi (1909) has shown that the gular crate, which he calls the "psammophore," is used as a basket in which to carry the sand and dust to the surface while the insects are excavating their burrows. Without such equipment the species nesting in dry sand or earth would probably find excavation extremely laborious and time-consuming, because the mandibles are not suited to the transportation of very finely-divided or powdery substances.

Besides the psammophore just described there are in certain ants other more important modifications of the head that may be interpreted as adaptations to the nonliving environment. The most conspicuous of these have evidently developed in response to the habitual contacts of the insects with the walls of their burrows, especially when they are tubular and excavated in solid wood. Similar and even more striking cases are well-known among both larval and adult beetles, notably among the Ipidæ, Platypodidæ, Bostrichidæ, Ptindæ, Cerambycidæ, etc. The insect, especially if it rotates while boring through the wood, makes a perfectly tubular gallery, in adaptation to which the body takes on a more or less perfectly cylindrical form. But since most ants, even many of the wood-boring species, have rather long, slender bodies, they need to acquire no special adaptive change in structure, though in some tropical species, and especially in the queens, the tenuity of the body may be greatly exaggerated. This is the case, e.g., in the Myrmicine *Pseudomyrma filiformis* (fig. 36) which, according to my observations, regularly inhabits the very narrow pith-cavities of a particular neotropical shrub. And in *Camponotus* (*Myrmostenus*) *mirabilis* (fig. 37) which belongs to a different subfamily, the Formicinæ, we find a very similar elongation of the head and body. The latter species is known only from single female specimens taken at lights, but there can be little doubt that its nesting habits are much like those of *Ps. filiformis*.

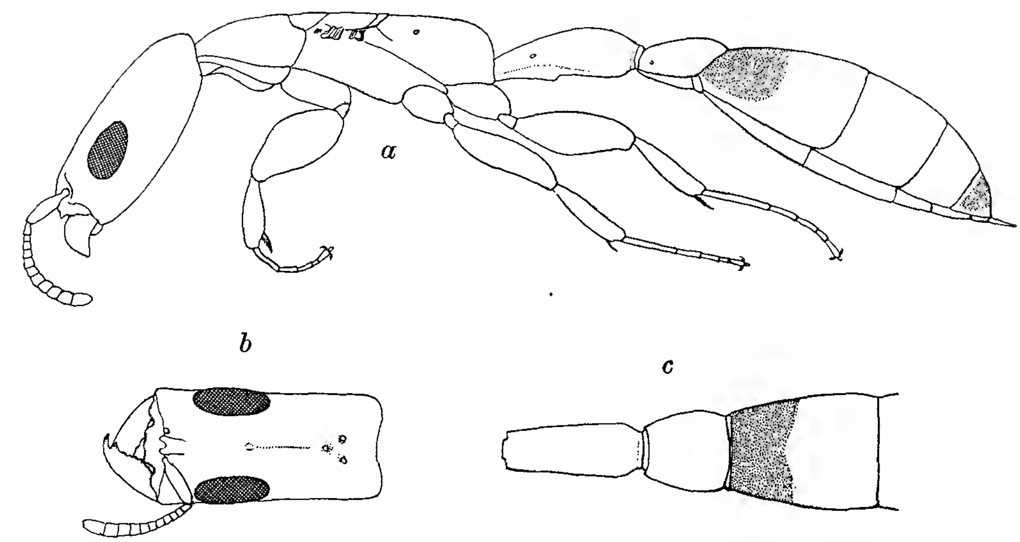

Fig. 36. A Neotropical Pseudomyrmine Ant, *Pseudomyrma filiformis* Fabr., Adapted to Living in Hollow Twigs

a, female (deälated) in profile; *b*, head of same from above; *c*, pedicel and first gastric segment from above

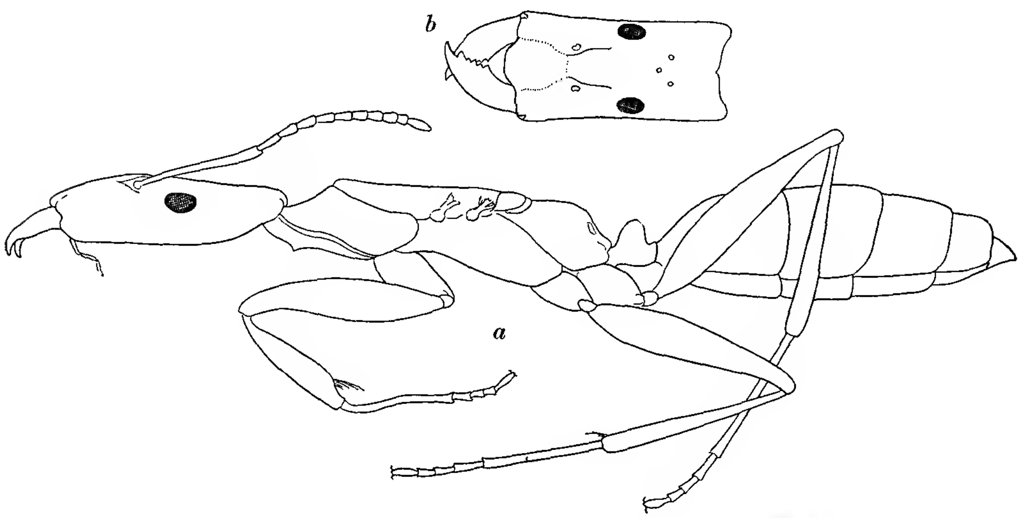

Fig. 37. *a*, Female (Dealated) of a Peruvian Formicine Ant, *Camponotus* (*Myrmostenus*) *mirabilis* Emery, Adapted to Life in Hollow Twigs; *b*, Head of Same from Above

PHRAGMOSIS

A more interesting adaptation to living in hard-walled, tubular cavities occurs in several genera, e.g., *Camponotus*, whose queens and soldiers have short, cylindrical and anteriorly sharply truncated heads, with the truncated surface circular, indurated and more strongly sculptured than the remainder of the body (fig. 38). These ants use the head, like the thick door of a safe, to close the entrance of the nest and keep out intruders. The nest which is excavated in hard wood, lig-

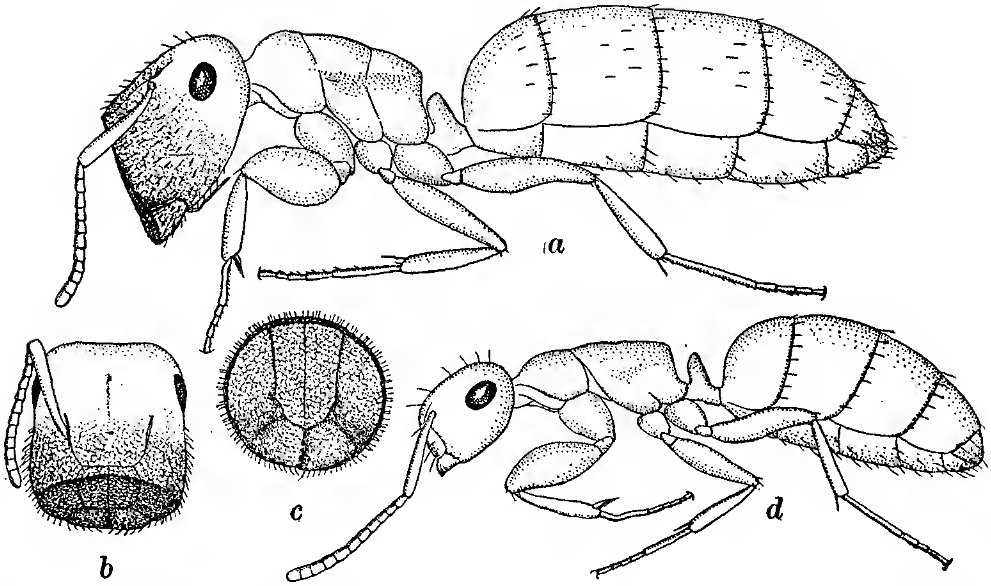

FIG. 38. *Camponotus* (*Colobopsis*) *etiolatus* WHEELER, A COMMON PHRAGMOTIC ANT IN THE LIVE OAK GALLS OF TEXAS

a, soldier; *b*, head of soldier from above; *c*, same directly from front; *d*, worker

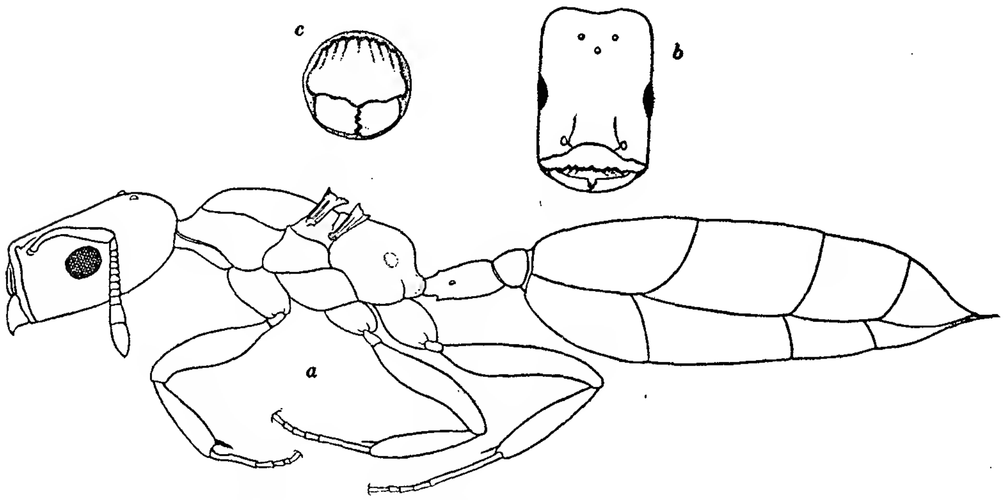

FIG. 39. *Crematogaster* (*Colobocrema* SUBGEN. NOV.) *cylindriceps* SP. NOV., A PHRAGMOTIC TWIG-INHABITING ANT FROM THE PHILIPPINES

a, female (deälated) in profile; *b*, head from above; *c*, anterior view of head

neous galls or the stems of rushes, has a perfectly circular entrance which is guarded by a soldier whose head exactly fits the orifice. When a worker desires to forage she strokes the soldier's abdomen with her antennæ and the animated door moves back and as soon as she has passed out of the nest returns at

once to its previous position. On returning she knocks with her antennæ on the exposed truncated surface of the janitor's head and a similar response permits her to enter. I find this same type of head in single exotic species of three other unrelated genera: *Pheidole*, *Crematogaster* (fig. 39), and *Epopostruma* (fig. 40), which, in all probability have much the same habits. There are also several lignicolous subgenera of *Camponotus* (*Paracolobopsis*, *Pseudocolobopsis*, *Manniella*, *Neomyrmamblys*) which exhibit similar modifications of the head in the queens and major workers. In some species of *Cryptocerus*, which also live in hard wood, the heads of the soldiers are broad and shield-shaped, and are also used for closing the nest-entrances.

The peculiar plug-like modification of the ant's head, like the scrobes, suggests an interesting problem which can be briefly discussed in this place. Very similar adaptations for closing the entrances to the burrows are found not only in a number of other Arthropods (e.g., in the termites of the genus *Cryptotermes*) but also in animals belonging to other phyla.

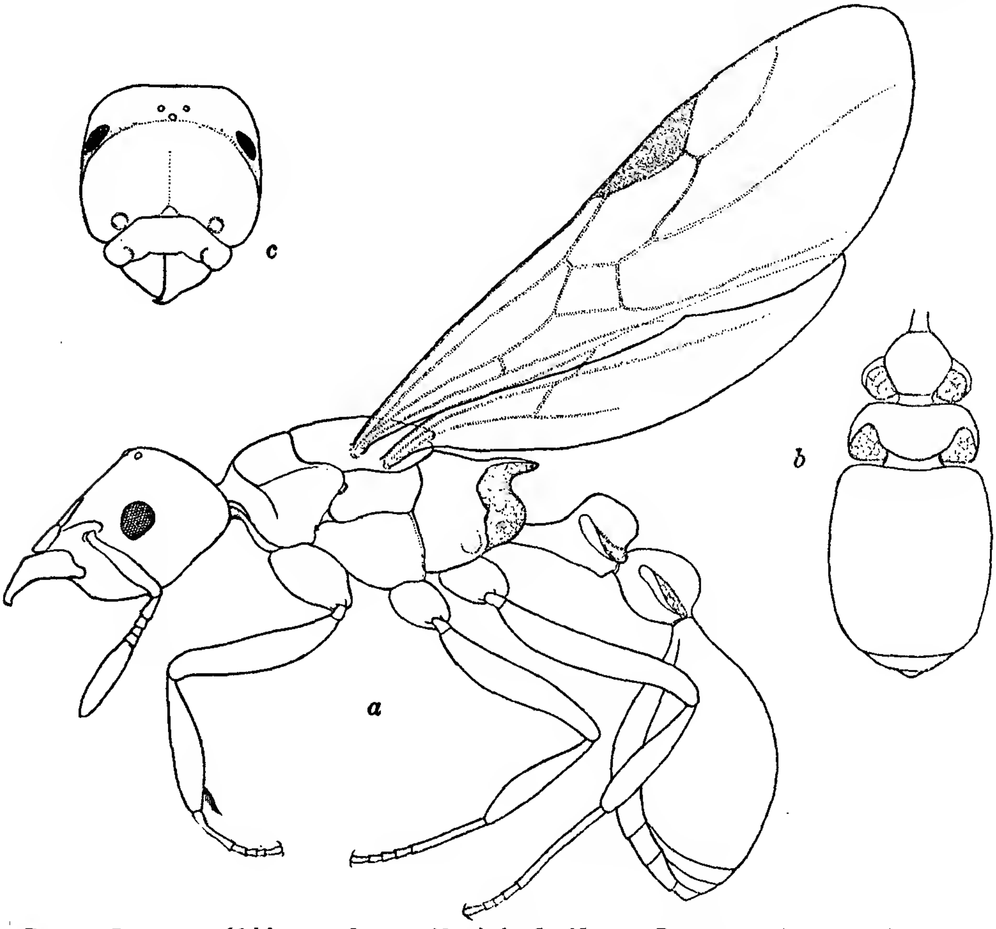

FIG. 40. *Epopostruma* (*Colobostruma* SUBGEN. NOV.) *lea* SP. NOV., A PHRAGMOTIC ANT FROM AUSTRALIA
a, female in profile; *b*, pedicel and gaster; *c*, head from above

In some cases the head, in others the posterior end of the body is adaptively modified, but in both instances the truncation, its circular outline and the hardening of its integument are strangely similar. Sometimes, as in the larvæ of tiger-beetles (*Cicindela*) and the burrowing bees of the genus *Halictus*, the whole head is nearly

Fig. 41. A Toad, *Bufo empusus* from Cuba, Which Closes Its Earthen Burrow with Its Hard, Shelly Head
(After T. Barbour)

circular and plug-shaped, in other forms, like the bark-beetles (Scolytidæ, Platypodidæ) and the caterpillars of *Circinnus melshaemeri* and *Perophora sanguinolenta* which inhabit tubular cases made of leaves, the posterior end of the body is sharply truncated and roughened or spinulate. A figure and description of the habits of *C. melshaemeri* is given in Harris (1862), while *P. sanguinolenta* is figured in Sharp (1899). I have observed the caterpillars of the latter or an allied species in British Guiana. In certain Annelids (Maldanidæ, Amphictenidæ) that live in tubular burrows, the head is hard and shelly. I reproduce Petrunkevitch's figure of a peculiar Theraphosid spider (*Chorizops loricatus*) (fig. 42) which, instead of making a trap-door like the allied species, uses the posterior end of its body for closing its burrow.

Barbour (1914, 1919, 1926) and Dunn (1926) have recently called attention to several interesting cases of the closure of burrows with modified heads and posterior ends in vertebrates. Barbour in his delightful book on reptiles and amphibians says: "It is well known that in many frogs the skin of the head becomes involved in the cranial ossification and becomes adherent, indurated, and rugose. This makes a hard bony head and should the frog back into a burrow it has but to tip his head down to close the entrance effectively. That this was ever regularly done on a large scale was never known until by chance, the author, after many long hunts for *Bufo empusus* in Cuba, chanced upon an open field over which were scattered many small burrows. These were evidently of two sorts, for the openings of some were carefully rimmed with smooth patted clay, while the others were rough and looked unfinished. Each of those with the rims contained one of the toads for which he had searched so long—the *sapo de concha* in Spanish—the shell-headed toad. These tube-like burrows were perfectly cylindrical, and perhaps seven to ten inches deep. The toad, which always looked larger than the burrow, when it was removed, was to be found near the bottom of the hole, the horn-like head forming a perfect operculum and perfectly fitting the caliber of the

tube." With Dr. Barbour's permission I reproduce his figure of this toad (fig. 41). Both he and Dunn have shown that a very similar closure of the burrow occurs in a number of wood inhabiting tree-frogs (e.g. in *Hyla lichenata* of Jamaica). In this connection Barbour also calls attention to two other groups of vertebrates in which the posterior end of the body is similarly employed, namely the snakes of the family Uropeltidæ, "where the head is sharp and the tail knobbed and shielded or even sometimes roughened," and certain small armadillos, of which he says: "Perhaps the most marvelous example of all is to be seen among mammals, in the two species of Pichiciegos of Bolivia and northwestern Argentine. These little armadillos of the genus Chlamydophorus burrow and live underground. Their body is nearly cylindrical, the head sharp and pointed, and the great fore limbs are mole-like in the extreme, but the posterior end of the body is as if sharply chopped off and is covered by a bony shield. This closes the burrow perfectly and no prying snake following its underground path could possibly get its jaws about it."

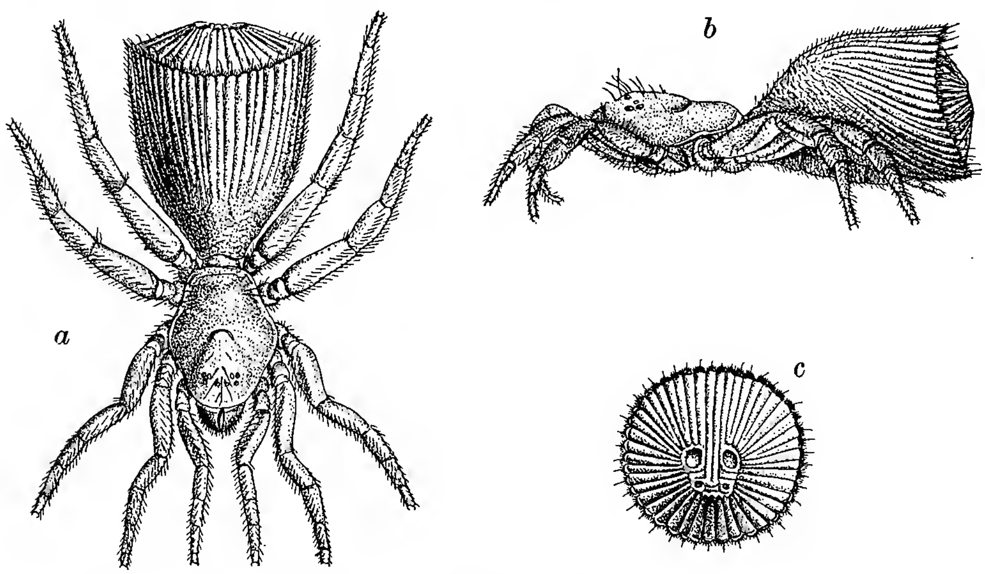

FIG. 42. A NEOTROPICAL SPIDER (*Chorizops loricatus*) WHICH CLOSES ITS BURROW WITH THE TRUNCATED POSTERIOR END OF ITS ABDOMEN

a, dorsal view; *b*, lateral view; *c*, truncated surface of abdomen. (After A. Petrunkevitch)

As there is no general term to cover all the peculiar, sporadic but convergent modifications of the ends of the body for closing tubular burrows I suggest the word "phragmosis," from φραγμός, a fence or barricade. From evolutionary and behavioristic points of view the phenomenon, as one of the most striking and definite methods of protection and defence, would seem to deserve more careful investigation than it has received. The phragmotic insect, instead of secreting or constructing a stopper, like the operculum or epiphragm of snails and the earthen or silken barricades or doors erected at the entrances of their burrows by many ants, wasps and trap-door spiders, actually employs for the purpose a specialized portion of its own body, thus affording a proof that no hard and fast line can be drawn

between behavioristic activities on the one hand and physiological and morphogenic processes on the other. The phylogenetic development of phragmosis is obscure. The ants, at least, seem to indicate that it cannot have arisen as a sudden, saltatory variation, but must have developed gradually, since we have among the many species of lignicolous *Camponoti* continuous series of approximations to the perfected condition observed in *Colobopsis* (fig. 38).

DETERMINATION OF SHAPE OF THORAX AND ABDOMEN

It will be seen from the foregoing discussion that the most important general factor in determining the shape and size of the head, at any rate in insects with biting mouthparts, is the flexor musculature of the mandibles. When we turn to the great motor region of the insect body, the thorax, the dependence of the size and shape of the skeleton on the volume of the leg and especially of the wing musculature, becomes even more manifest. Attention has been so often directed to this matter, that little remains to be said about it. Such insects as the aphids show the correlation very clearly during their post-embryonic instars, but the various castes even of a single species of ant, furnish an even more impressive illustration. In worker ants, which never develop wings, save as rare, pathological vestiges, the thorax is greatly simplified in structure and diminished in size as compared with the thorax of the winged castes; and among the queens of certain species (*Leptothorax emersoni*) we discern a gradual reduction in its size and complexity as we pass from the macrothoracic, winged individuals, through steno- to microthoracic, apterous forms essentially like the workers. That the development of the wing-muscles very largely determines the size and shape of the thorax is also revealed by a comparative study of insects like the Odonata, Hymenoptera, Diptera and Coleoptera, in which the relative volumes of the meso- and metathoracic segments are clearly correlated with the relative size and efficiency of their respective pairs of wings.

The physiognomy of the insect abdomen, however, is not determined so much by the development of the musculature of the various segments as by the volume of the viscera, i.e., the alimentary canal, reproductive organs and fat-body. The phenomenon of "physogastry," or hypertrophy of the abdomen is in some cases due to an enormous increase in the contents of the crop, as in the honey-ants, in others to enlargement of the ovaries or fat-body, as in the aged queens of termites and certain ants (*Dorylinæ*, *Anergates*) and the various termitophiles of the more extreme type (*Corotoca*, *Spirachtha*, etc.). This physogastry is really of considerable physiological interest but its adequate consideration would unduly expand this article.

In conclusion we may revert briefly to some of the general types observed in man—the dysplastics, giants, dwarfs and acromegalics. Stockard has shown that very similar types may be clearly recognized among the various breeds of dogs, such as the St. Bernard (acromegalic), bull-dog (achondroplastic dwarf), black-and-tan (ateleotic dwarf), etc. Many cases of giantism and nanism might be cited among the insects, and among the dwarfs the soldiers of certain ants (*Pheidole*, *Acanthomyrmex*, etc.) are in many respects strangely analogous to the achondroplastics (fig. 21*a*), while the small workers (fig. 21*f*) are even more like the ateleotics. The development of these forms evidently depends on both genetic

and endocrine factors but the proportional intervention and interrelation of these factors have not been established. Owing to lack of knowledge of the precise functions of the various glands which in insects might be regarded as analogous to the endocrine glands of vertebrates, we are unable to frame any satisfactory physiological explanation of the Hexapod dwarfs. If certain ants have really learned to produce achondroplastics and ateleotics *ad libitum* and to turn over to them the main asexual activities of the colony, we should have another fine example of the extraordinary ability of insects to exploit to the utmost everything in their environment. As yet man has learned to employ his achondroplastics, ateleotics and other dysplastics only as court pets, court jesters and circus freaks.

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